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Population Dynamics and Ecophysiology of Fraser fir (*Abies fraseri*) in the High Elevation Forests in the Southern Appalachian Mountains

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To the Graduate Council:

I am submitting herewith a dissertation written by Steven Douglas Kaylor entitled "Population Dynamics and Ecophysiology of Fraser fir (*Abies fraseri*) in the High Elevation Forests in the Southern Appalachian Mountains." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

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Population Dynamics and Ecophysiology of Fraser fir (*Abies fraseri*) in the High Elevation Forests in the Southern Appalachian Mountains

A Dissertation Presented for the
Doctor of Philosophy
Degree
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Steven Douglas Kaylor

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Dedication

Dr. Tom Pauley once told me our job as biologists
is to speak for the things that had no voice,
to be their mouthpiece in the world of men.
To the voiceless, I dedicate mine.

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Though our cultural image of a scientist is one of a lone explorer making discoveries, science is truly a collaborative effort, and there are a number of people who supported, helped and guided me throughout my graduate career and the completion of my dissertation research. First and foremost, I am thankful to Joe Hughes for his continual support, both as my husband and the other half of the forest disturbance ecology lab.

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Abstract

Dominated by the endemic Fraser fir (*Abies fraseri*), the high-elevation forests of the Southern Appalachians are one of the most endangered ecosystems in the United States, and the future of these forests remains uncertain. Fraser fir is showing signs of decline in health and increased mortality throughout its range, possibly due to multiple environmental stresses.

Using twenty years of forest monitoring data, this dissertation documents change in forest structure and species composition in high-elevation red spruce-Fraser fir forests in southern Appalachia and generates predictions of future forest change. Additionally, it quantifies physiological measures of carbon fixation, storage and growth in adult Fraser fir *in situ* under multiple stresses, which has been unstudied previously, and explores environmental constraints associated with climate, soil chemistry and acidic deposition on physiological metrics.

We find no evidence of previously hypothesized shifts in forest composition to greater dominance of northern hardwood species across elevation and nitrogen deposition gradients or between different initial stand types. Using a stage-structured Bayesian hierarchical model to predict Fraser fir populations through 2050, we predict robust recovery of populations on Clingmans Dome and Mount LeConte for at least the next several decades, as well as continued decline for populations on a number of mountains, notably Mount Sterling at the lowest end of Fraser fir's elevation range. We find that maximum photosynthetic rates are low throughout the high elevation mountains of Great Smoky Mountains National Park, indicating trees are under considerable stress, but are highest in trees growing on the highest, steepest slopes. Trees from Clingmans Dome have significantly higher maximum photosynthetic rates and water use efficiency than trees on other mountains, which may indicate stress resistance in this population. Additionally both photosynthetic water use efficiency and leaf architecture are affected by maximum July temperature, suggesting future climate change will impact the foliar physiology of Fraser fir. Measurements of nonstructural carbohydrate pools are consistent with those found in mature trees of other species which suggests the capacity for resistance of future stress events, particularly at the highest elevations where photosynthetic rates are the highest.

Preface

29 June 0627
The cold mountain fog makes coffee
a necessity. Firs the color of smoke in the early
Dawn light. I stumble toward the spring.
Water, the life blood pouring out of
the rocks of Mount Uyaye,
Guardian Mountain of the Cherokee.
Going to the Water, the first people's
Holy Rite.

I, too, am rising early, going to the water.
Cleansing, invigorating, icy water--
Though pure no longer.
When did filtration become essential on this
holy mount? Are the spirits still here,
or have they left the land,
tainted by smog and ozone?
A single snake shed,
improbable in this altitude,
holds my answer.
A sign and a gift in the stiff dawn.

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Chapter 1
Introduction

1.1 A Review of Relevant Literature

1.1.1 Natural Variation within Species

Intraspecific natural variation, broadly defined as the within-species phenotypic variation in a given trait or parameter, is ultimately caused by spontaneously arising mutations that have been maintained by artificial and natural selection. The amount of intraspecific variation in key physiological traits like specific leaf area and leaf gas exchange measures varies by species (Poorter et al. 2009, Wilson et al. 1999, Abrams 1994). However, variation in physiological measurements across a landscape is unknown with regard to many species, and this variation is an important consideration when trying to assess the future outlook of individuals of threatened species.

Partitioning how much of this variation in physiological measures are due to phenotypic plasticity in response to environmental conditions versus genetically controlled traits is difficult (Ackerly et al. 2000), but informs some of the most fundamental current questions in ecology (Sutherland et al. 2013). Plants have a remarkable ability to alter their development in response to numerous environmental cues and stresses. A host of environmental cues can be interpreted by plants, including light, temperature and nutrients, and these inputs are integrated and translated into a range of developmental outputs like shoot elongation, leaf architecture, photosynthetic pigment production, and biomass allocation (Gratani 2014, Caldwell and Pearcy 1994). This plasticity enables growth optimization for the local environment, allows range expansion into heterogeneous habitats, and may provide an advantage as the changing climate affects growth conditions around the globe. Individual trees can show a tremendous ability to acclimate to a changing environment, with the magnitude and variability of this response dependent upon species (Larigauderie and Körner 1995; Tjoelker et al. 1999), provenance (Bigras 2000; Gunderson et al. 2000), elevation (Fryer and Ledig 1972), and other factors. Genetic variation is fundamental for the persistence of a species because it provides the short term acclimation potential of an individual to the current biotic and abiotic conditions as well as providing diversity for long term adaptation in response to selection (van Delden 1994). If the genetic structure within a species or population is compromised due to population reduction and isolation, then the stability of the forest ecosystem may also be reduced when faced with future environmental changes (DeHayes et al. 2000).

Additionally, unusually harsh or extreme environments provide an understanding of the limits of plant growth and function and the process of plant adaptation and distribution patterns. Measurements of photosynthesis, temperature, water and nutrient relations provide the foundation for understanding adaptations in physiological processes and can provide insights into the responses of plants to a changing world. Studies of water relations and drought stress in the harsh deserts of the southwest have helped elucidate the processes by which tree mortality occurs under such extreme conditions (Sevanto et al. 2013, McDowell & Sevanto 2010), and the adaptations which allow individuals to acclimate to drought conditions (McDowell et al 2008). Conversely, studies in the high elevation cloud forests of the Great Smoky Mountains will provide insight on tree water usage and foliar light response (Berry & Smith 2012, 2013, Reinhardt & Smith 2008), and carbon gain and allocation in locally adapted conifers, which is especially relevant to understanding future impacts of changing climate on boreal forests.

1.1.2 Biogeography and Evolution of Fraser fir

The genus *Abies* is a group of 37-48 species generally restricted to cool and frigid environments in the northern hemisphere, with a few lower latitude species that persist only in high elevation ecosystems (Liu 1971). One of these lower latitude species is Fraser fir (*Abies fraseri* (Pursh.) Poiret). Fraser fir is the dominant tree species in the high-elevation forests of the southern Appalachian Mountains. This endemic conifer is found in island-like populations in seven locations in Tennessee, North Carolina and Virginia from 1,767 to 2,037 m in elevation (Beck 1990). The species natural elevation range is above 1,300 meters where it is co-dominant with red spruce (*Picea rubens*), and becomes the dominant tree species above about 1,800 meters (Cain 1935; Whittaker 1956; Busing et al. 1993). Adult Fraser firs range in size from 9 to 25 m tall, with most individuals around 15-18 m tall and under 30 cm D.B.H. (Beck 1990). Fraser fir generally reaches maturity and begins reproducing around 40 years of age and has a natural life span of about 150 years (Oosting & Billings 1951)

Fraser fir is thought to be a relict population of a large conifer forest that once covered as much as 1.8 million km^2 of the southeastern United States (Delcourt & Delcourt 1984; Delcourt & Delcourt 1998) in the late-Wisconsin glacial period, from 18,000 years to 12,500 years before present (Whitehead 1973; Whitehead 1981; Delcourt & Delcourt 1987). This forest retreated

northward as climatic warming occurred and became the Canadian boreal forest, leaving only refugial, disjunct populations at the higher elevations in the Southern Appalachians about 8,000 years ago. Recent studies have shown close genetic similarities with the balsam fir (*Abies balsamea*) which is found extensively in the northern latitudes of the northeastern US and Canada and the Canaan fir (*Abies balsamea* var. *phanerolepis*) endemic to West Virginia and Virginia (Potter et al. 2010a) and suggest they became genetically isolated from each other 7,000-10,000 years ago (Clark et al. 2000). The genetic structure of Fraser fir populations shows a significant deficiency of heterozygosity and a high degree of inbreeding relative to other conifers (Potter et al. 2008). This may have implications for the degree to which Fraser fir is able to acclimate or adapt to environmental and biological stresses.

1.1.3 Southern Appalachian Spruce Fir-Spruce Forests

Though the southern Appalachian spruce-fir forests have historically been regarded as an extension of the boreal forest (Whittaker 1956; Ramseur 1960), there are notable differences between the two ecosystems. Vegetation in the high-elevation spruce-fir forests is a mixture of boreal relicts and montane species (White 1984; Wiser 1994). Additionally, southern Appalachian spruce-fir forests receive greater annual precipitation, in amounts up to 2,500 mm per year (Shanks 1954). Much of this precipitation is from clouds; cloud immersion occurs in these forests 65% of all days annually (Mohnen 1992; Baumgardner et al. 2003) and about 30% of typical summer day (Reinhart & Smith 2008). Therefore, spruce-fir forests in the southern Appalachians are a unique ecosystem--a high-elevation temperate cloud forest.

These forests are noted for their relatively high level of endemic species and relict populations of species only found in coniferous forests at much higher latitudes, especially in the pure fir of the highest peaks (Nicholas et al. 1999). A study of plant occurrences in the spruce-fir forest of the Great Smoky Mountains National Park found 132 species of vascular plants, 8 of which are endemic, and 6 are thought to be relict populations isolated from northern forests (White 1984). In addition, Fraser fir is the preferred host for 36 species of bryophytes (Smith 1984) and 20 species of epiphytic lichen (Dey 1984). Several bird species restricted to higher elevations depend on spruce-fir canopy including the black-throated green warbler, blue-headed vireo, red-breasted nuthatch and golden-crowned kinglet, and their numbers have been significantly reduced following the BWA infestation (Rabenold 1998). Of the species found

in Fraser fir forests, twenty are federally listed as "of concern" including two federally listed endangered species, the spruce-fir moss spider (*Microhexura montivega*) and the Carolina Flying Squirrel (*Glaucomys sabrinus coloratus*).

The current geographic distribution of Fraser fir covers about half of what it once was in the late nineteenth century (Dull et al. 1988). Logging and failed regeneration caused by site degradation and poor management practices dramatically reduced the range of Southern Appalachian spruce- fir in the early 1900s (Pyle & Shafale 1988; Pyle 1984). With the establishment of Great Smoky Mountains National Park in 1934, protection of the largest part of this montane ecosystem was assured (Dull et al. 1988). Today most of the extant spruce fir forests in southern Appalachia is on public lands; indeed Fraser fir and the spruce-fir ecosystem is a central attraction of several well-known tourism destinations in the southern Appalachians like the Great Smoky Mountains National Park, Mt. Mitchell State Park, Grandfather Mountain private reserve, and Roan Mountain (in the Pisgah National Forest). Though these forests are protected from further anthropogenic disturbance, they are showing signs of decline in health and vigor potentially caused by multiple environmental stresses.

1.1.4 Tree Stress

Plant stress is defined as sustained deviation of any environmental condition beyond the optimum range which reduces plant potential productivity. There are several stresses associated with the high-elevation forests that have been identified over the last few decades. The relevant literature on these individual stresses and their effects of fir physiology is reviewed below.

1.1.5 Atmospheric Deposition

The major effects of long-term acid deposition on soils include accumulation of sulfate and nitrate, increased solubility and mobilization of aluminum, and depletion of nutrients like Ca, K, and Mg. Spruce-fir forests in Great Smoky Mountains National Park are currently classified at a stage 2 of nitrogen deposition (*sensu* Aber et al.1998) and receive a moderately high amount of nitrogen with wet, dry and fog deposition totaling about 30 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Johnson et al.1991; Lovett & Lindberg 1993). Much of this N is leached from the soil, with rates as high as 20 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Nodvin et al. 1995). As soil N levels increase, Fenn et al. (1998) predict a change in

forest type, where slow growing, slow N cycling conifer species are out-competed by deciduous maples and birches which can take advantage of the increased N.

In addition, Fraser fir has been shown to have preferences in nitrogen form. A study comparing response to fertilization by either NO_3^- or NH_4^+ found that young trees were able to use NO3- as a sole nitrogen source. Nutrient uptake (N, P, K, Ca and Mg) and photosynthetic capacity both decreased with increasing proportion of NH_4^+ application (Rothstein & Cregg 2005). Reports of amounts and relative proportions of these two N forms in red spruce-Fraser fir forests conflict, but all report high levels of overall N accumulation (Sasser & Binkley 1988; van Miegroet et al. *1993*).

The relatively thin, acidic soils of the high elevation forests offer limited buffering capacity for increased acidity (Shubzda et al. 1995). Increased soil acidity has been shown to lower cation exchange capacity and also results in the conversion of Aluminum into soluble forms that may be then taken up by plants. Studies of foliar elemental composition in both Fraser fir and the co-dominant red spruce have shown considerably elevated levels of Al as well as low Ca:Al ratios (Robarge et al. 1989). Aluminum severely impacts root growth in plants, reducing root mass and thus nutrient and water uptake. The most toxic soluble form, Al^{3+}, inhibits cell division, cell extension, and transport within the cell (Kozlowski & Pallardy 1997). Increased soluble aluminum also results in loss of essential nutrients from the soil; it is able to displace Ca, K, and Mg from soil cation exchange sites. These displaced minerals are then subject to leaching and become limiting nutrients for plant growth. Fine root turnover has been shown to be higher at sites with higher soil Ca availability, and cation depletion associated with acidic deposition has been suggested to cause reduced carbon allocation to fine roots in spruce-fir ecosystems (Park et al. 2008).

In addition to changes in soil chemistry and nutrient dynamics, acid deposition impacts Fraser fir through cloud deposition and acid fog. High elevation forests receive about half of their considerable annual precipitation (> 2000 mm per year) from cloud water deposition and spend roughly a third of the summer immersed in clouds (Reinhart & Smith 2008b). Increased exposure to acid fog causes decreases in Ca and Mg within tissues by increasing foliar leaching (Shepard et al. 1995, Joslin et al. 1988). In red spruce, low amounts of foliar calcium have been linked to significant increases in dark respiration (MacLaughlin et al. 1991). Repeated exposure to acidic rain with high sulfur content causes needle necrosis, early senescence and defoliation

(Jacobson et al. 1990). Recent findings by Wilson and Butcher (2012) have found higher foliar concentrations of Ca and Mg than earlier studies, indicating that pollution controls may be limiting foliar leaching. However, high pollution levels in the Great Smoky Mountains may be also contributing to forest decline through lowered photosynthesis by reducing leaf chlorophyll content, and causing increased winter damage through lack of hardening (Adams & Eager 1992).

1.1.6 Ozone

Ground level ozone amounts in the Great Smoky Mountains National Park are among the highest in the eastern US (Mueller 1994, US EPA 2001). On average, ozone concentrations over the ridge-tops of the park are twice that of nearby Knoxville and Atlanta. From 1997 to 2010 there were over 500 days over 75 ppb, and 264 of these days had ozone levels over 85 ppb (US NPS 2010). High elevation ecosystems are thought to be particularly vulnerable to increased ozone pollution; ozone levels do not decline at night in these areas so they receive a higher amount of exposure for a longer period of time (Adams & Eager 1992). Ozone enters stomata and reacts with lipid and protein components of leaf tissue to form aldehydes, peroxides and various reactive oxygen species (ROS). These substances cause reduced stomatal conductance and photosynthesis, trigger the creation of antioxidants and even stimulate programmed cell death (Andersen 2003; Wittig et al. 2009). In sensitive species, long-term exposure leads to reduced growth rates and early leaf senescence (Somer et al.1998; Karnosky et al.2005).

Though increased tropospheric ozone has been shown to have deleterious effects on some conifer species (Benoit et al. 1982; Woodman 1987), Fraser fir does not appear to be ozone sensitive. A study of the effect of long-term ozone fumigation on Fraser fir seedlings found no effect on seedling growth. Seedlings exhibited no consistent change in leaf net photosynthesis, stomatal conductance and total biomass when exposed to ozone concentrations as high as 0.15 ppm during five accelerated 10-week growth cycles (Seiler et al. 1994). Studies have also found no interactive effects of water stress and increased ozone on Fraser fir photosynthesis, respiration or conductance (Tseng et al. 1988).

1.1.7 Elevated Atmospheric CO_2

In addition to increased atmospheric deposition and ground level ozone amounts, burning fossil fuels and release of stored carbon into the atmosphere have led to greater levels of

atmospheric CO_2. CO_2 levels have increased by about 70ppm in the last 50 years and it is predicted that CO_2 will continue to rise over the next few decades. A study of the effect of elevated CO_2 on Fraser fir seedlings found that plants exposed to elevated CO_2 (712 ppm) for a year were significantly larger in dry weight and size than those grown at ambient (374) but had lower water use efficiency, conductance, and photosynthetic rates (Samuelson & Seiler 1992). A similar study of red spruce found seedlings exposed to the same elevated CO_2 level during budset and subjected to water stress had greater leaf weight, leaf area and height of the terminal leader than the control. Red spruce seedlings grown for 5 months at 712 ppm CO_2 were taller, had denser canopies, and more biomass than those grown at ambient (Samuelson & Seiler 1994).

With elevated CO2, trees will be able to open their stomata for shorter periods of time and acquire more carbon for growth and storage, which may also make them less vulnerable to stress in drought conditions. However, increases in growth rates may lead to increased competition pressures for nutrients, water and space. Elevated atmospheric CO_2 is also predicted to cause changes in global temperature with an estimated increase in global mean annual temperature of 3 C in the next 100 years.

1.1.8 Climate Change

Delcourt and Delcourt (1998) predict that a 3 C increase in the mean July temperature would raise climatically-limited ecosystems about 480 m in elevation. Because red spruce-Fraser fir forests are already confined to the highest mountain elevations, this shift could result in loss of the ecosystem. However, trees at high elevations may be able to acclimate or develop adaptation to increased temperatures. A study of elevated warming on red spruce found varying response to increased temperatures among different seed sources, indicating that temperature alone is unlikely to limit future establishment and growth (Hagen 2006). Potter et al. (2010b) developed an empirical multivariate clustering algorithm to predict future suitable habitat of individual tree species based on environmental characteristics existing at current locations. Using the higher emissions estimate published by the Hadley Centre for Climate Prediction and Research in this algorithm, predicted suitable habitat of Fraser fir in the southern Appalachians will shrink over the next 40 years but by 2100 will expand to a similar extent to current habitat. These results do not take into account changes in precipitation or cloud cover,

or potential physiological adaptations or acclimation to changes in climate. Additionally, because these models are based on current species distributions, which is biased by human land use change, they may under-predict species resilience to climate change.

Along with a mean annual temperature increase, changes in precipitation patterns in the southeastern United States are also being anticipated. Fraser fir grows in a cold, moist climate characterized as a cool-temperate rain forest with a well-distributed mean annual precipitation of 1900 to 2540 mm (Beck 1990). Because it is adapted to such a wet environment, Fraser fir is susceptible to stress caused by lack of water availability. One study found three year old seedlings subjected to moderate water stress (watered when pre-dawn needle water potential was between −0.8 and −1.0 MPa) showed a 20% reduction in root and shoot dry weight as well as a decrease in both transpiration and leaf conductance. Seedlings subjected to severe water stress showed improved water use efficiency which may indicate acclimation to drought periods is possible (Tseng et al. 1988). In more recent study, water stress in four year old Fraser fir seedlings significantly impacted height growth, relative root collar diameter and terminal shoot growth and caused decreased levels of end-of-season leaf pigments. However, drought stress had no significant effect on leaf carbohydrate levels, suggesting that the effects seen on plant growth were not a result of carbon starvation but hydraulic failure (Kulak et al. 2012). This may be because the plant compensates by ensuring an increase in the relative availability of resources for root development as evidenced by a higher ratio of leaf N to root weight (Nzokou & Cregg 2010).

Reinhart and Smith (2008b) found that leaf conductance of understory *Fraser fir* decreased exponentially as the vapor pressure difference between the leaf and atmosphere increased. A rise in vapor pressure difference from 0 to 0.5 kPa resulted in an 80–90% reduction in conductance. In addition, cloud saturation led to increases in light saturated photosynthesis (Reinhart & Smith 2008a). The ecotone between the spruce-fir zone and the southern hardwood forests roughly corresponds with the beginning of cloud immersion, and spruce-fir forests spend 30-40% of the growing season immersed in clouds (Reinhart & Smith 2008b). Cloud immersion has been shown to result in higher photosynthesis rates, leaf conductance and xylem water potentials in sapling Fraser fir (Berry & Smith 2013), but this impact has been shown to be greater on juvenile than adult trees (Berry & Smith 2012). This effect is not due to however to differences in stomatal pattern or frequency between high and low elevation individuals, but is

probably due to resource partitioning and use efficiency (Reed & Smith 2012). Because global climate change is predicted to increase regional cloud ceiling levels, it is expected that the negative impacts on Fraser fir physiology associated with coming out of cloud immersion will drive the optimal habitat for the species higher in elevation.

1.1.9 Balsam Woolly Adelgid

One of the most devastating stresses on Fraser Fir in the last century has been from predation by an invasive insect, the balsam woolly adelgid (*Aldeges piceae* Ratz.). A native of European silver fir forests, BWA was introduced into Maine and Nova Scotia on nursery stock in 1908 (Hain 1988). It was first discovered in the red spruce-Fraser fir forest in Mt. Mitchell, North Carolina in 1955, and the Great Smoky Mountains National Park in 1960. BWA is able to reproduce parthenogenetically and lays about 100 eggs with about 3 generations produced each year (Balch 1952; Amman & Speers 1965; Eagar 1984). The adelgid feeds on phloem by inserting its stylus-like mouth in the bark fissures of older fir trees, mainly those over 4 cm DBH (Eagar 1984).

In response to adelgid infestation, changes in both the phloem and xylem tissues of Fraser fir occur. Parenchyma form around the site of the stylus; these parenchyma subsequently degrade and are filled with resin and enclosed in cork tissue. This layer may help prevent against subsequent infestation. In the xylem, short heavily-lignified trachids are produced (Eager 1985). The response-wood is anatomically similar to compression-wood and heartwood. Depredation by BWA may also increase lower xylem pressure potentials and lead to cavitation of sapwood. The decrease of functioning xylem tissue lowers water conductance below critical levels and the tree succumbs to mortality in 2-3 years (Hollingsworth et al. 1991).

While as much as 90% of over-story Fraser fir died during the height of the infestation (Dull et al. 1988), a few individual mature trees remain. Reasons for their survival are unclear, but there are a few hypothesized mechanisms of resistance. Grand fir (*Abies grandis*) produces copious amounts of resin as a wound response and is fairly resistant to adelgid attack with only 20-30% of infested trees dying (Mitchell 1966). Resin contains many secondary metabolites and helps prevent infestation and damage by insects, fungi and pathogens; greater resin production may be a trait that assists in resisting BWA depredation. Natural variation in bark thicknesses or xylem anatomy may also increase the possibility of survival. Hollingsworth and Hain (1994)

hypothesize that low mortality rates of Fraser fir at Mount Rogers, Virginia may be caused by greater water availability at that site. Fowler et al. (2001) suggest that the juvenile hormone related compound Juvabione, which is produced in young trees, may be higher in resistant individuals.

1.1.10 Multiple Stresses

None of these environmental and biological stresses happen alone. Competition pressures from elevated CO_2 levels add to those caused by N accumulation. Nitrogen deposition may also influence herbivory, and may affect tree drought- and cold-tolerance through alterations to tree anatomy and carbon allocation. Changes in global climate will impact soil nutrient cycling and availability (Garten 1999). Trees infested by BWA seem to be less resistant to drought stress because they continue to produce abnormal wood growth even with reduced water availability (Hollingsworth & Hain 1994).

Under field conditions tree responses can be synergistically or antagonistically modified by the superimposition of other stresses. Synergistic effects could be additive or multiplicative; trees may react in a non-linear way to perturbations, such as climate change, so that the outcome may be greater than the sum effect of the individual components (Aber et al. 2001).

Down-regulation of photochemistry and, in the longer term, of carbon metabolism is an important defense mechanism in response to environmental stress. Changes in the root:shoot ratio or in nutrient reserve partitioning are accompanied by alterations in nitrogen and carbon metabolism. At the whole tree level, stresses may result in the slowing of growth and/or the decline of carbohydrate reserves. This creates a complex system of stress interactions and tree physiological and ecological response that will drive the future of the species.

1.1.11 Growth and Phenology of Fraser fir

Though an understanding of the growth and phenology of Fraser fir is essential to making accurate predictions about response to stress, particularly climate change (Rossi et al. 2011; Kramer et al. 2000), the timing of annual events related to growth and function in Fraser fir remains largely unstudied. Studies of the timing of bud break and primary growth in adult firs have been confined to the closely-related northern species balsam fir. Generally, fir bud break is determined by mean daily temperature, the threshold of which varies by population and

elevation. A study of plantation-grown balsam fir in Northern Michigan in 2000 found bud break began in most adult trees between 78-105 degree days above 10 C (April 22 to May 3) (Fondren & McCullough 2003) while observations of the same species from 1979 in Quebec placed bud break between 194 -215 degree days above the threshold of 4 C (Osawa et al.1983). Subalpine (*A. lasiocarpa*) and Pacific silver (*A. amabilis*) firs in Washington have been shown to exhibit variation in threshold temperatures as well, with seedlings at higher elevations flushing earlier by about 7 days per 1000 m difference (Worrall 1983). The lone study of seedling phenology in Fraser fir, however, found the opposite. Though bud break was determined by mean daily temperature, higher parent elevation was associated with later terminal and lateral bud flush dates and slower growth rates in seedlings (Emerson et al. 2006). While earlier flushing in northern latitudes may be adaptations to compensate for shorter growing periods, these adaptations may not be necessary in the southern Appalachians. Here, the later flushing dates likely developed to prevent frost damage of new shoots.

Secondary growth of adult Fraser fir is again unexamined, but fairly well studied in balsam fir. In a study of xylem phenology in adult balsam fir in Quebec in 1998 to 2000, cell formation began between May 7 and June 7. The transition between earlywood and latewood production occurred between July 2 and July 19, and the end of the growing season was observed between August 20 and September 20 (Deslauriers et al. 2003a). Studies of cambial activity in both roots and stems of balsam fir in Quebec show similar initiation and conclusion dates for growth with similar variation (Thiebault-Martel et al. 2008). Temperature is the main factor driving xylogenesis during spring, and variations between these dates are hypothesized to be caused by year to year and site to site variations in climate. Short-term variations in temperature have been found to influence cell production or stem radius increase in many boreal and high-altitude coniferous species (Deslauriers et al. 2003b, Deslauriers & Morin, 2005, Rossi et al. 2011). Rossi et al. (2006) have also posited day length as a further important factor for onset of growth in coniferous species. An average annual temperature increase of 4 C predicted over the next century could stimulate earlier needle flush in Fraser fir, leaving trees vulnerable to damage by frost (Emerson et al. 2006). Earlier bud break may also increase vulnerability to insect attacks by aphids or spruce budworm (Fondren & McCullough 2003). At the same time, an increase in daily temperatures would create a longer growing season and

possibly increased primary and secondary growth of trees and greater fecundity (Rossi et al. 2011).

1.2 Research Objectives

The studies presented here document change in forest structure and species composition in high-elevation southern Appalachian spruce-fir forests, quantify physiological measures in adult Fraser fir under multiple stresses, and generate predictions of future forest change. Additionally, they provide a basic understanding of adult Fraser fir physiology in natural stands, which was found to be absent in the literature, identify possible genetic resources in fir relevant to survival of chronic environmental stresses.

Chapter 2 exploits the long-term monitoring dataset to evaluate hypotheses about forest change and dynamics in response to chronic environmental stress and large severe selective disturbance. It was hypothesized that hardwoods were increasing in high-elevation forests due to 1.) alterations in nutrient dynamics caused by high nitrogen deposition 2.) shifts in local temperatures, which should be noticeable at lower elevations 3.) exploitation of canopy gaps caused by insect induced fir mortality. We find no support for any of these hypotheses; data instead suggests alternative based on Grimes C-S-R triangle.

Chapter 3 again uses the long-term monitoring dataset to ask whether Fraser fir forests are recovering from large scale mortality and what can we expect in the future for fir populations. We first generate size curves that describe changes in fir forest structure throughout the study over the last twenty years and the current state of fir populations. Then we make a stage structured population model using Bayesian methods to predict fir population densities through 2050.

Chapter 4 quantifies physiological measurements associated with carbon fixation and allocation in adult Fraser fir occurring in natural stands. Then the relative importance of environmental factors of temperature, growing season, soil nutrient content, soil water availability, and acid deposition rates on fir physiology are explored. To determine possible future effects of climate warming, fir physiological metrics are viewed in terms of temperature or elevational gradients. Physiological metrics were also compared between mountain populations to identify possible genetic differences.

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Appendix

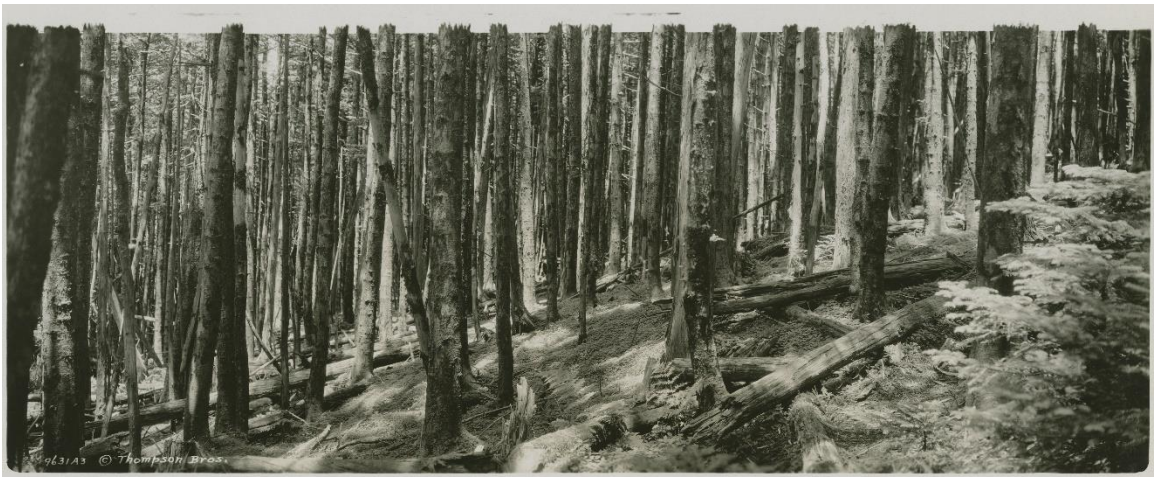

Figure 1.1. Fraser fir forest on Mount Leconte, early 1930's. Photograph by the Thompson Brothers. http://dlc.lib.utk.edu/thompson/thompson_entry.htm

Figure 1.2. Spruce-fir forest on Mount Sterling looking toward Mount Guyot, 1930's. Photograph by Herbert Webster. http://digital.lib.utk.edu/collections/webstercollection/

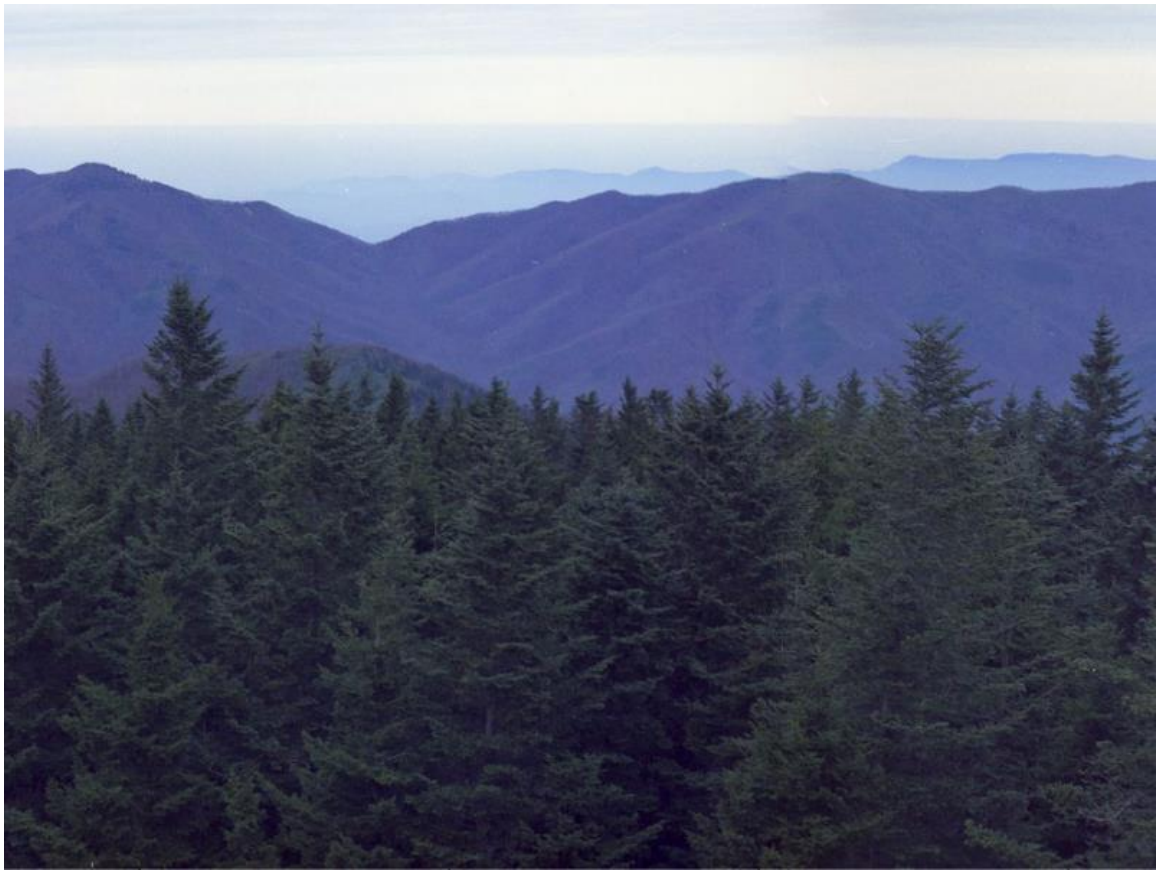

Figure 1.3. High-elevation spruce fir forest in Great Smoky Mountains National Park, pre-adelgid. Photograph by Elgin Kinter. http://digital.lib.utk.edu/collections/kintnercollection/

Figure 1.4. Dead and regenerating Fraser fir (*Abies fraseri*) on the summit of Clingmans Dome, 2010. Author's photograph.

Figure 1.5. High-elevation spruce fir forest on the summit of Mount LeConte, 2012. Authors photograph.

Figure 1.6. Mature Fraser fir near the summit of Mount Rogers, VA, 2006. Note wide canopy and high needle density. Photograph by Kevin Potter.
http://repository.lib.ncsu.edu/ir/handle/1840.16/5794

Figure 1.7. Typical mature Fraser fir near the summit of Mount LeConte, 2012. Note extremely reduced canopy, and low needle density. Author's photograph.

Chapter 2

Evaluating Hypotheses of Species Shifts in High Elevation Southern Appalachian Forests Following Long Term Stress and Severe Disturbance

This chapter was submitted to Vegetation Science in July 2015 as a research article by myself, M. Joseph Hughes, and Jennifer Franklin. I formulated the questions, performed the research, and was the primary author of the manuscript.

Abstract

Questions: This study examines questions relevant to previously hypothesized shifts from cool temperate coniferous forests toward greater hardwood composition: 1) Are changes in forest type occurring at lower ends of elevation gradients as a consequence of range shifts anticipated as a result of climate warming? 2) Are increases in hardwoods correlated with nitrogen deposition rates, offering support for hypothesized effects of soil nitrogen saturation in forest ecosystems? 3) Is increase in hardwood dominance greater in forest stands that had greater hardwood composition directly following a selective disturbance that caused severe conifer mortality? *Location:* These hypotheses are addressed in the high elevation *Picea rubens-Abies fraseri* forests of the Southern Appalachian mountains. The study was carried out in 37 long-term monitoring plots located over 5 mountains in Great Smoky Mountains National Park. *Methods:* Data from two decades of monitoring was analyzed to determine the change in hardwood share in both the overstory and sapling class from 1990 to 2010. These values were regressed against modeled annual plot N deposition values and plot elevation to determine the respective influence of N deposition and climatic gradients on changes in forest type. Additionally, we compare changes in hardwood share in both size classes between plots which were mostly fir and those which were mixed species in 1990. *Results:* Our study finds no evidence that a shift in forest composition to greater dominance of northern hardwood species is occurring and no support for previously hypothesized changes across elevation and nitrogen deposition gradients. Further, there is no statistical difference between forests which were mostly fir and those with a greater hardwood component at the beginning of the study. Findings suggest both recruitment of *A. fraseri* into the overstory and trade-offs in hardwood species with different life history strategies are occurring. *Conclusions:* We conclude that neither long-term stress from climate and anthropogenic N saturation, nor *Abies*-selective disturbance are primaries drivers of change in tree communities in these forests.

2.1 Introduction

Disturbance and environmental stress are selective pressures which can change the forest types that exist in a given location (Fralish & McArdle 2009; White et al. 2012). Post-disturbance change in species composition is a result of different evolutionary strategies that are reflected in plant functional traits related to resource capture, regeneration, and growth (Bernhardt-Römermann et al. 2011; Raevel et al. 2012; Wilfahrt et al. 2014). In the case of the *Picea rubens-Abies fraseri* forests of the southern Appalachians, which occur in a small number of island-like populations at the highest elevations, it has been suggested that selective disturbance pressures may drive the forest from one dominated by the endemic *Abies fraseri* and *Picea rubens* toward one with a greater presence of deciduous trees (Delcourt & Delcourt 1998; Fenn et al. 1998; Smith & Nicholas 1998). There are a number of disturbance factors which could be responsible for composition shifts, and given the minimal direct human disturbance in this area, three are likely to be particularly important: changes in climate, high nitrogen deposition rates, and selective insect depredations. Though these disturbances may affect a number of different forest types world-wide (Iverson & Prasad 2001, Peñuelas & Boada 2003, Ellison et al. 2005, Hamann and Wang 2006, Beckage et al 2008, Bobbink et al 2010, Zhuang et al. 2014), the high-elevation forests of the Southern Appalachian Mountains are distinctively positioned to examine potential effects on shifts in forest type from these three disturbances.

The Southern Appalachian spruce-fir forests represent the southern end of the spruce-fir forest type, which extends northward and forms the Canadian boreal forest. As such, they may be particularly vulnerable to climate warming. Temperature shifts associated with climate warming are hypothesized to shift optimal habitat for *A. fraseri* toward higher elevations or more northern latitudes (Solomon 1986; Bugmann & Solomon 1995; Delcourt & Delcourt 1998). A 3 C increase in mean July temperatures could raise the lower bound of *A. fraseri* habitat by 480 m in elevation or about 2.8 northward in latitude (about 310.8 km) by the end of the century (Delcourt & Delcourt 1998). Conservative estimates for climate shifts in the next 70 years predict a 3 C average increase in annual temperatures in the Southeastern US (Karl et al. 2009). Greater changes may mean local extirpation or extinction of climatically-limited high-elevation species. In fact, climate warming is already underway; from 1970-2008 the mean annual temperature in the southeastern U.S. has increased 0.9 C (Karl et al. 2009). Climate envelope models based on temperature, precipitation, topography and growing season for *A.*

fraseri predict a niche contraction over the next forty years, which will then stabilize by the end of the century (Potter et al. 2010). This contraction may reduce *P. rubens-A. fraseri* forest coverage at the lower bound of its elevation range, and this niche may then be filled by existing and adjacent species.

Nitrogen deposition in these high elevation forests is also hypothesized to result in a shift in species composition (Aber et al. 1989; McNulty et al. 1996; Fenn et al. 1998). Southern Appalachian *P. rubens-A. fraseri* forests are nitrogen saturated; total deposition levels have been measured at about 30 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Johnson et al. 1991; Lovett & Lindberg 1993, Weathers et al. 2006). However, nitrogen deposition effects on tree communities, especially with regard to different life history strategies, are still poorly understood (Wilfahrt et al. 2014). Chronically elevated N deposition in forest communities is predicted to cause a dramatic increase in the availability of NO_3- accompanied by a change in N dynamics toward a rapid movement of NO_3- within forest soils (Aber et al. 1989; Stoddard 1994). Sustained N saturation is also hypothesized to lead to declines in net primary productivity (Aber et al. 1989; Fenn et al. 1998). Increased N mobility may favor certain plant species that are able to quickly use available N to generate biomass. Preferential acquisition and use of NO_3- vs. NH_4+ differs between plant species and across ecological succession, with species characteristic of late-successional habitats and/or those on strongly acidic soils having been shown to have strong preferences for the NH_4+ form (Zak & Pregitzer 1990; Lavoie et al. 1992; Kronzucker et al. 1997; Ste-marie & Pare 1999). Continued soil nitrogen saturation of a decade or more has been shown to cause imbalances in foliar nutrients and may contribute to successional changes from a slow growing and slow N-cycling coniferous forest, to a fast N-cycling and fast growing deciduous forest (McNulty et al. 1996; Fenn et al. 1998; Barker et al. 2002; McNulty et al. 2005).

Finally, a third recent major disturbance to high-elevation forests is the creation of canopy gaps by widespread mortality of overstory *A. fraseri* (DeSelm & Boner 1984; Smith & Nicholas 1998). Depredation by an invasive insect, *Adelges piceae* (Hollingsworth & Hain 1991), killed an estimated 91% of mature *A. fraseri* in the overstory during the height of the infestation in the 1970's and 80's (Dull et al. 1988). Under its natural disturbance regime, Fraser fir is a shade-tolerant slow-growing species which normally exhibits advanced recruitment beneath a closed canopy (Oosting & Billings 1951). With the decimation of mature fir populations, this recruitment pattern may have been broken, allowing species with intermediate shade tolerance

or shade intolerance to become established. Forest stands with a greater mix of species prior to disturbance may have had greater propagule pressure from surviving mature hardwoods, while stands in which *A. fraseri* was dominant had greater resources become available when the overstory canopy died. The presence of hardwood seed in the seed bank and arriving through wind dispersal may be greater at the lower end of the elevation range closer to the ecotone with the hardwood forest.

The two broad species groups of interest have different life-history tradeoffs in carbon allocation strategies and plant functional traits (Reich et al. 1998; Landhäusser & Lieffers 2001). Many conifers are slow-growing and take longer to mature than deciduous trees; their strategy is one of stress tolerance, prioritizing carbon expenditure for maintenance and persistence on the landscape. In contrast, the most common deciduous trees that occur in high-elevation forests (*Sorbus americana, Betula alleghaniensis, Prunus pensylvanica,* and *Acer spicatum*) have rapid growth and maturity, indicating a prioritization of carbon toward growth and reproduction (Grime 2001). We expect these two strategies to provide different advantages under different environmental conditions and disturbance agents and intensities. Conifers like *P. rubens* and *A. fraseri* have long-lived tissues and low productivity which allows for resistance where growth is limited by adverse conditions like low light availability, short growing seasons, or low rates of mineral nutrient supply, but this strategy does not allow for quick reproduction after a major disturbance like fires or insect outbreaks. Hardwoods, by contrast, may fare better in these post-disturbance scenarios where rapid resource capture and the proliferation of offspring are successful strategies.

We analyzed data from two decades of monitoring to examine possible changes in composition of high elevation forests to a type more dominated by hardwoods. We evaluated changes in forest composition to answer the following specific questions: 1) Are changes in forest type occurring at lower ends of elevation gradients as a consequence of range shifts anticipated as a result of climate warming? 2) Are increases in hardwoods correlated with nitrogen deposition rates, offering support for hypothesized effects of soil nitrogen saturation in high-elevation ecosystems? 3) Lastly, is increase in hardwood dominance greater in forest stands which had greater hardwood composition in 1990 after experiencing high overstory *A. fraseri* mortality, and does this relationship differ by elevation?

2.2 Methods

2.2.1 Study Area

The study was carried out in the Great Smoky Mountains National Park (GSMNP), which contains 74% of the nearly 36,500 ha of extant *P. rubens-A. fraseri* forests (Dull et al. 1988). Five mountains, encompassing nearly the entire *A. fraseri* range in the GSMNP, were chosen for study areas in 1990: Mount Sterling, Mount Guyot, Mount LeConte, Mount Collins and Clingmans Dome (Figure 2.1). Study area elevations range from 1,722m on Mount Sterling to 1,999m on Mount LeConte.

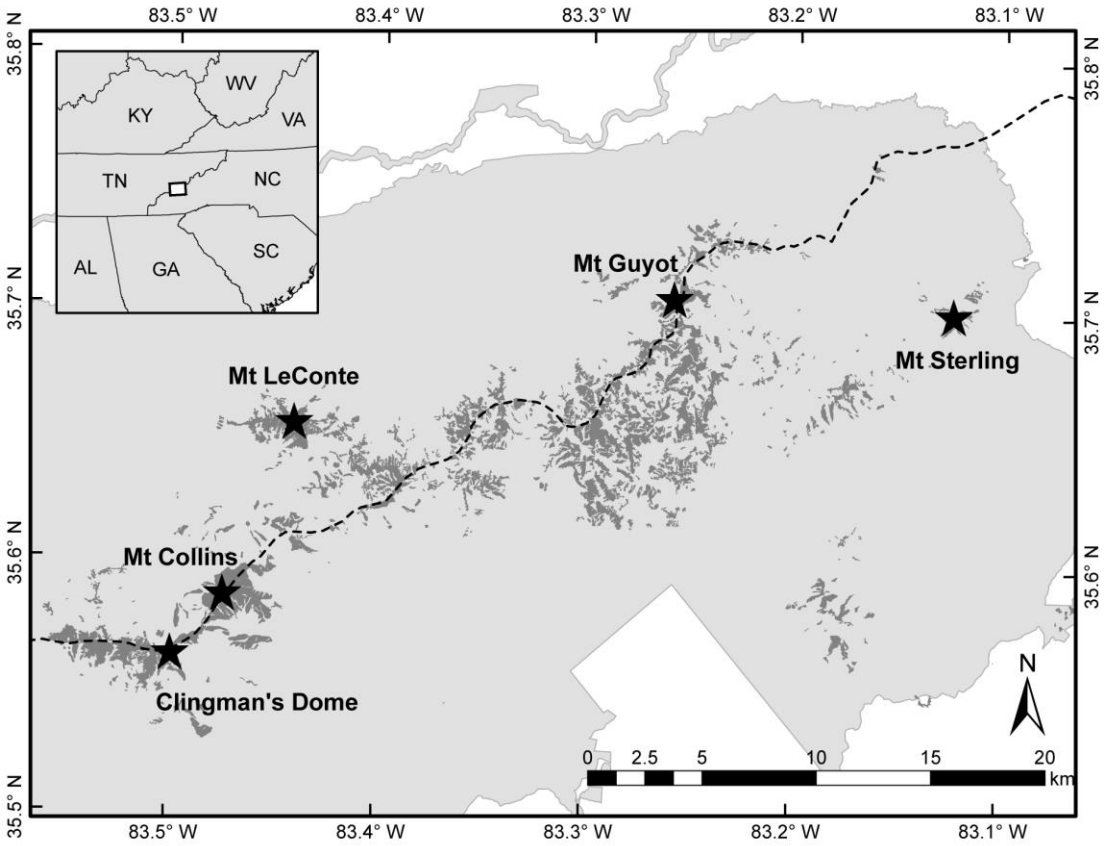

Figure 2.1. Research plot locations in Great Smoky Mountains National Park. Lightly shaded areas show park boundaries, while darkly shaded areas show *Picea rubens-Abies fraseri* forest cover within the park. There are 37 plots scattered over the 5 mountains indicated with a star. Plots measure 20 m x 20 m, are situated on different aspects, and range in elevation from 1721.7 m on Mount Sterling to 1999.3 m on Mount LeConte.

2.2.2 Data Collection

Thirty-seven long-term monitoring plots were established on these mountains in 1990 by National Park Service (NPS) as a replicated series of stratified plots with two replicates of four stand types on each site. These four stand types were based on both the intensity of Fraser fir mortality and dominance in the overstory at the time of plot establishment. These initial stand conditions provide a way to examine the effect of an initial condition on changes in forest species composition (Smith & Nicholas 1998; Smith & Nicholas 2000; Mancusi 2004). They are based on basal area measurements at the time of plot establishment: pure live fir (≥65% overstory of fir, ≥65% of fir living), pure dead fir (≥65% overstory of fir, ≥65% of fir dead), mixed live fir (≤35% overstory of fir, 65% of fir living), and mixed dead fir (≤35% overstory of fir, ≥65% of fir dead). Two plots on Mount Sterling and one plot on Mount Guyot were unable to be replicated due to a lack of stands of the given type on the mountain. Because plots which were mostly live fir in 1990 have experienced increased fir mortality in the ensuing decades, the present study only examines differences in hardwood encroachment with respect to overstory composition (mixed species vs. pure/mostly fir). None of the areas have been previously logged or burned; plots were old-growth fir forests before the widespread mortality event (Pyle 1984). Plots measure 400 m^2 and are situated on different aspects and elevations.

Forest plots were measured over the summers of 1990 and 2000 by NPS staff, and 2010 by D. Kaylor and NPS staff. The same written protocol and data sheets were used during each data collection period to minimize differences in sampling between periods. All live and dead overstory trees (>5 cm) were counted by species, mapped, tagged, and trunk diameter measured at 1.37 meters. Saplings (>1.37 m tall and <5 cm DBH) were determined to species and tallied in twelve 2 × 2 m subplots. Subplots were placed along 3 transects each randomly located in one of three pre-chosen plot quarters; four subplots were measured along each transect.

Because forests consist of a finite amount of resources shared by individuals, we use proportion of plot basal area as a proxy for resource competition (Opie 1968; Biging & Dobbertin 1996; Greene et al. 2002). Changes in overstory hardwood share between collection periods was calculated using basal areas between 1990 and 2000 and between 2000 and 2010; these were used in all analyses. Analyses using change in the share of hardwood stem count yielded similar results; only analysis using basal area are presented. Because resource competition is generally thought to be highest in the sapling size class where trees compete for

light and available nutrients (Kobe 1996; Finzi & Canham 2000), changes in sapling hardwood share were also examined.

2.2.3 Overall trends

To determine whether the overall proportion of hardwoods increased or decreased over the study period, average change in hardwood share from 1990 to 2010 for both the overstory and sapling class were calculated and assessed with Welch's one sample, two-tailed t-test. To examine possible differences in advantages of different life-history strategies, we look at basal area of 5 most common hardwood species through the study period. Because the time since disturbance differs by mountain (Smith & Nicholas 1998), we compare changes in hardwood share between mountains using Welch's ANOVA (Welch 1951).

2.2.4 Elevation/climate effects

To test whether plots at lower elevations are increasing in hardwood proportion as a hypothesized response of climatically limited forests to changes in climate, we used ArcMap (10.1, ESRI) to generate plot elevation from GPS coordinates taken at plot center. The changes in hardwood share over the two decades of monitoring in both saplings and overstory trees were used in a linear regression against these plot elevations.

2.2.5 Nitrogen Deposition

To address questions about the influence of long-term nitrogen saturation on changes in forest species composition, nitrogen deposition estimates were generated using a spatially explicit empirical model (Weathers et al. 2006). Using 378 point measurements and corresponding landscape variables throughout GSMNP, Weathers and colleagues constructed a general linear model relating deposition index to landscape variables measured in the field in 2000. Then, using the independent landscape variables available in GIS data layers, they created a GIS-relevant statistical nitrogen (N) and sulfur (S) deposition model (LandMod), which was validated using field data. This model provides average annual nitrogen deposition (wet + dry) estimates at a 30 meter spatial resolution.

We used plot locations to generate an estimate of average annual nitrogen deposition rate for each plot. While the highest deposition rates are seen at high elevations and lowest rate at the lowest elevation plots, this relationship is not strictly linear, indicating that aspect, terrain,

and forest type play a large part in nitrogen deposition rates (Weathers et al. 2006). Because of this non-linear relationship, we analyzed the effect of nitrogen deposition separately from that of elevation. A linear regression was used to test the relationship between changes in hardwood share over the two decades of monitoring in both saplings and overstory trees and annual nitrogen deposition rates.

2.2.6 Effects of Initial Conditions

Our final question was to examine whether forests which had greater hardwood composition in 1990 are experiencing increases in hardwood dominance and whether this relationship is greater in lower elevations, which may have greater propagule pressure of species from the adjacent northern hardwood forest type. We use the initial stand conditions described at the time of plot establishment (pure fir plots vs mixed fir plots), in an ANCOVA with plot elevation as a covariate to test these relationships.

All statistical testing was performed using MatLab (2014A, MathWorks, Inc.).

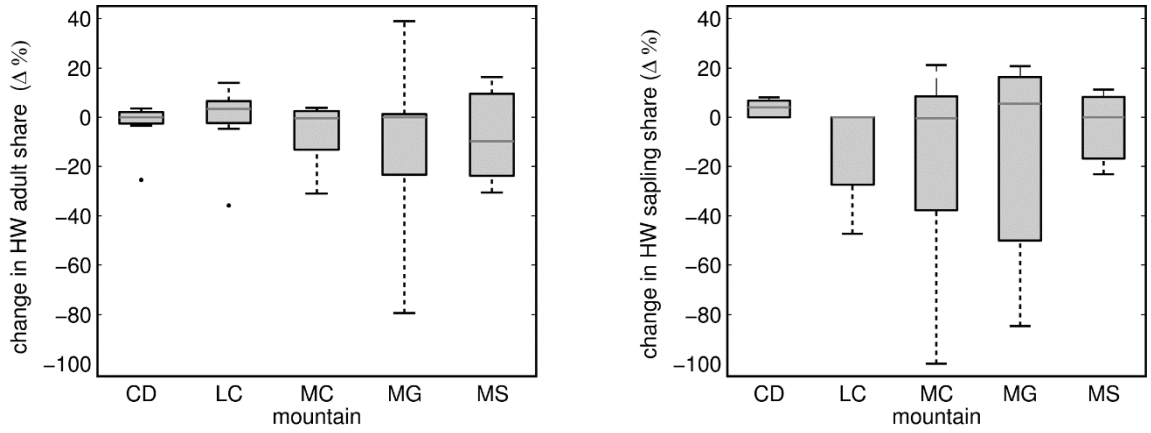

Figure 2.2. Change in hardwood share in overstory BA (left) and sapling density (right) from 1990-2010 in 37 long-term *Picea rubens-Abies fraseri* monitoring plots grouped by mountain in Great Smoky Mountains National Park. The central mark represents the median value, edges of the box are the 75th and 25th percentiles, whiskers extend to the most extreme values that are not outliers; outliers are defined as points that fall outside of +/- 1.5 times the interquartile range.

2.3 Results

2.3.1 Overall Trends

Plots in the high-elevation forests in Great Smoky Mountains National Park showed an average 5% decline (SEM= 3.32) in the overstory hardwood share over the last two decades (Welch's t-test, p=0.057). The changes in individual plots ranged from a 79% decrease to a 38% increase (Figure 2.2). In 43% of plots, hardwoods declined over the study period while 46% of plots showed some increase; the remaining 11%, representing 4 plots, were pure coniferous forests in both measurement periods. There is no statistical difference between mountains with respect to the average change in the overstory hardwood share, though plots on Mount Guyot exhibit the widest variance and account for both the greatest increases and decreases in hardwood share of overstory trees (Figure 2.2).

Examining changes in the hardwood share of the sapling class, overall the plots showed a significant decline in hardwood composition of saplings, with an average decline of 9% over all plots (SEM = 4.94) (Welch's t-test, p=0.035).Values for individual plots ranged from 100% decline in hardwood saplings to a 21% increase in the proportion of hardwood saplings. Of all forest plots sampled, 34% showed an increase in hardwoods in the sapling class while 32% showed declining ratios. Again, we find no statistical difference between mountains with respect to the average change in the hardwood share in the sapling class (Figure 2.2).

While total hardwood basal area throughout the study area remained relatively constant over the two decade period, overstory co-dominant *P. rubens* have declined slightly and *A. fraseri* basal area increased dramatically (Figure 2.3).

The most common hardwood species in the overstory of plots are shown in Figure 2.4. Seven species occurring within the study plots had less than 10 individuals observed in total over all monitoring plots, so are not represented. Over the sampling period we see a decline in *Prunus pensylvanica* and *Fagus grandifolia*, while *Betula alleghaniensis* and *Sorbus americana* increase slightly across all plots. *Acer spicatum* and *Quercus rubra*, which both represent smaller portions of the forest community, double in total basal area over all plots during the study period.

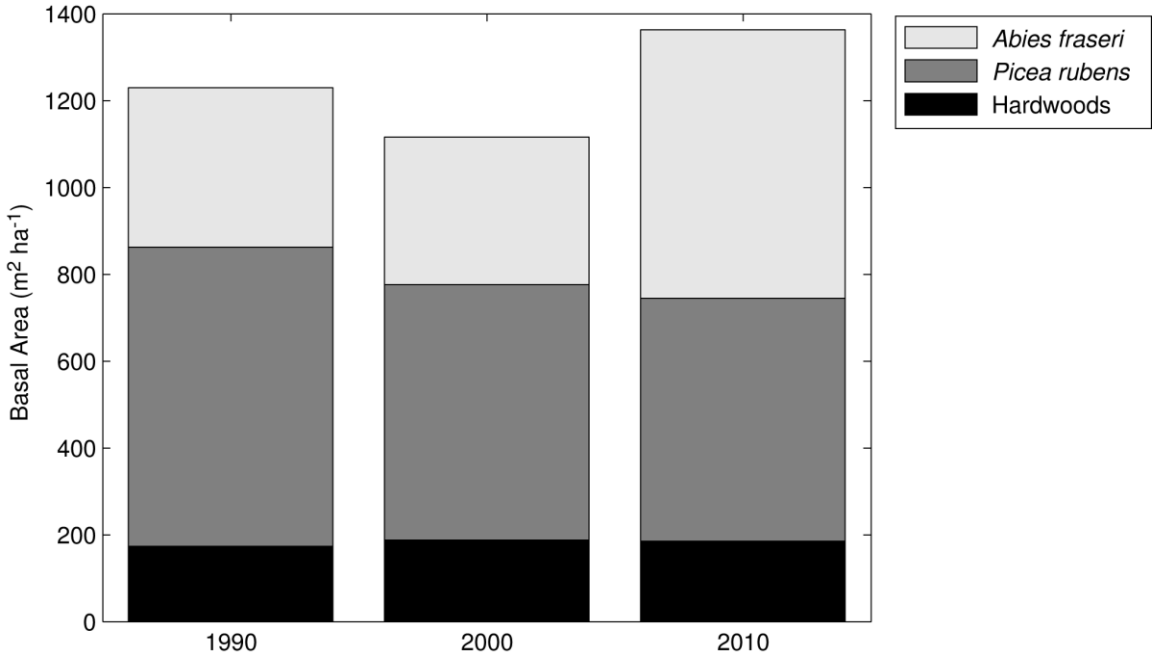

Figure 2.3. Total combined forest basal area in 37 long-term *Picea rubens-Abies fraseri* monitoring plots in Great Smoky Mountains National Park in 1990, 2000, & 2010. Proportion of *Abies fraseri*, *Picea rubens*, and mixed hardwoods is shown.

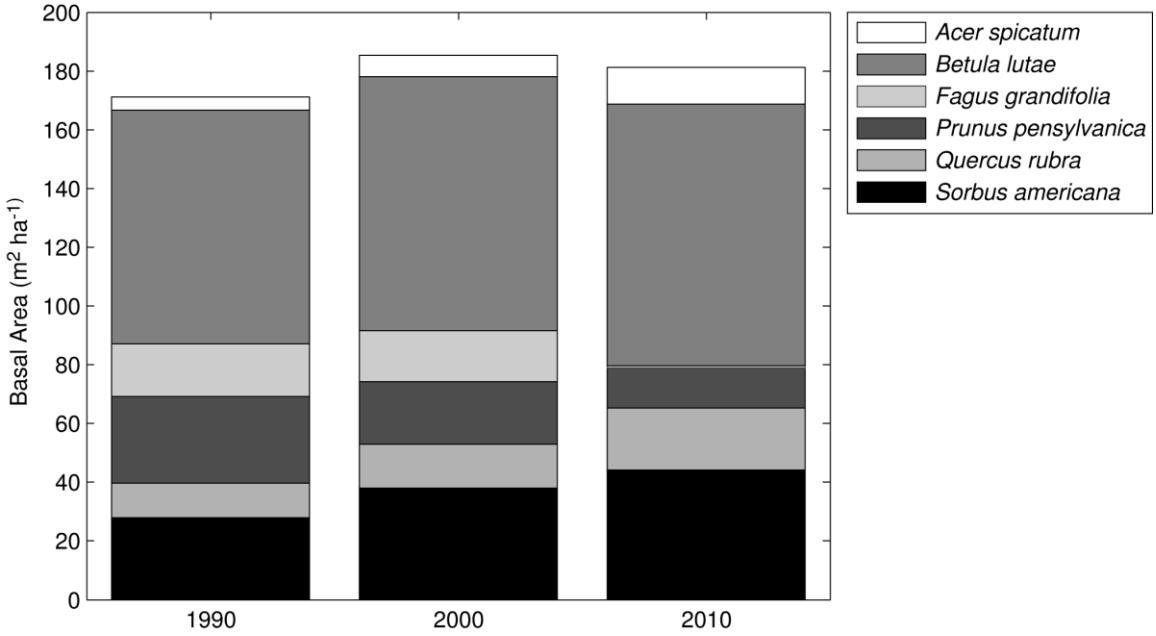

Figure 2.4. Total combined forest basal area in 37 long-term *Picea rubens-Abies fraseri* monitoring plots in Great Smoky Mountains National Park in 1990, 2000, & 2010. Proportion of *Sorbus americana*, *Quercus rubra*, *Prunus pensylvanica*, *Fagus grandifolia*, *Betula alleghaniensis* and *Acer spicatum* is shown. Species with >10 individuals total are omitted.

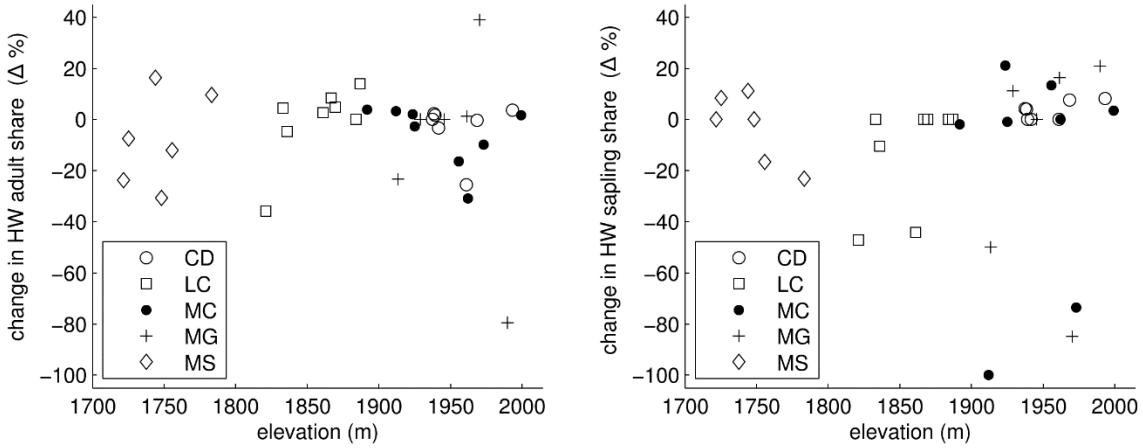

Figure 2.5. Change in hardwood share in overstory BA (left) and sapling density (right) from 1990-2010 regressed against elevation (m) in 37 long-term *Picea rubens-Abies fraseri* monitoring plots in Great Smoky Mountains National Park. Symbols represent plots on Clingman's Dome (CD – open circle), Mount LeConte (LC – open square), Mount Collins (MC – closed circle), Mount Guyot (MG – cross), and Mount Sterling (MS – open diamond).

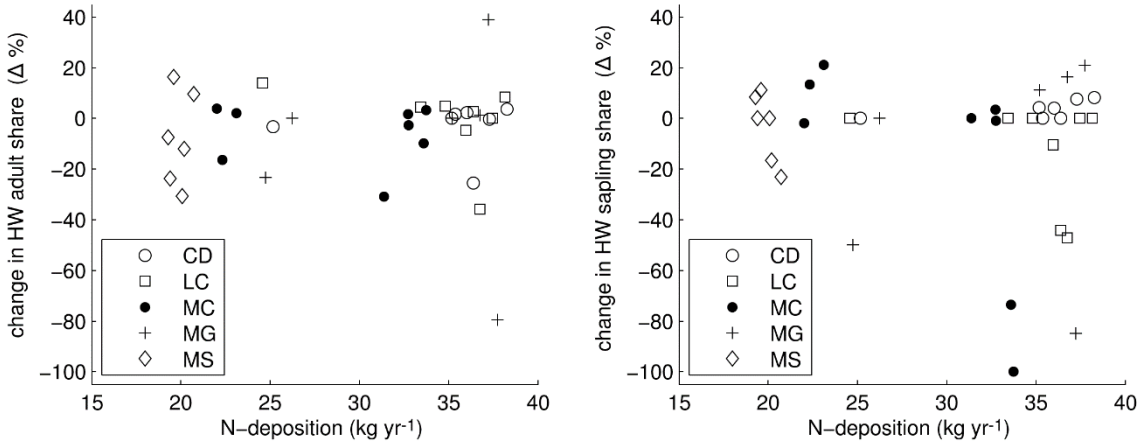

Figure 2.6: Change in hardwood share in overstory BA (left) and sapling density (right) from 1990-2010 regressed against N deposition estimates (kg/yr) from the Weathers et al. 2006 model in 37 long-term *Picea rubens-Abies fraseri* monitoring plots in Great Smoky Mountains National Park. Symbols represent plots on Clingman's Dome (CD – open circle), Mount LeConte (LC – open square), Mount Collins (MC – closed circle), Mount Guyot (MG – cross), and Mount Sterling (MS – open diamond).

2.3.2 Effects of elevation

The changes in overstory hardwood share in individual plots ranged from a 79% decrease to a 38% increase, but the majority of plots showed less than a 20% change. Changes in hardwood share of saplings were comparable. Across an elevational rise of 300 m, regressions show no significant relationships between this hardwood change and elevation in either size class. Even the lowest elevation plots on each mountain do not exhibit increases in hardwood share over the study period (Figure 2.5).

2.3.3 Effects of Nitrogen deposition

Total annual N deposition estimates ranged from 19.2 to 38.2 kg · yr^{-1}. However, there is no statistically significant relationship between changes in hardwood share in either the overstory or sapling size classes with respect to the estimated annual N deposition amount (Figure 2.6). Some plots which experience N deposition in excess of 30 kg · yr^{-1} show large declines in hardwood saplings over the twenty years of study.

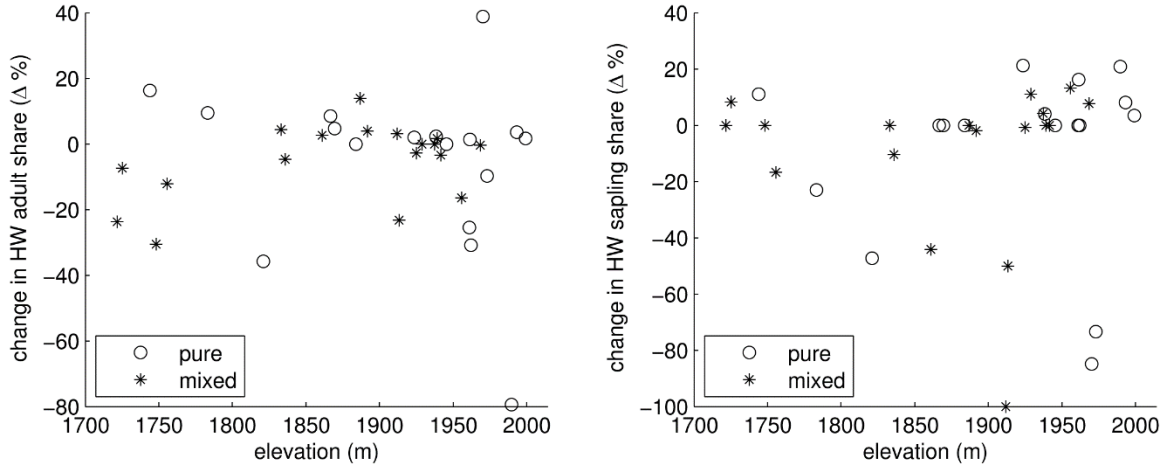

Figure 2.7. ANCOVA showing effect of elevation on change in hardwood share in overstory BA (left) and sapling density (right) from 1990-2010 in 37 long-term *Picea rubens-Abies fraseri* monitoring plots in Great Smoky Mountains National Park. Symbols represent initial stand conditions in 1990 at the time of plot establishment: plots with overstory composition greater than 65% fir in 1990 ("pure"- open circles) and those that were less 35% fir ("mixed" - asterisk). Elevation regressions were non-significant.

2.3.4 Effects of initial stand composition

Finally, we compared change in hardwood share between plots which were *A. fraseri* dominated overstory in 1990 with those that were dominated by other species in 1990. Because of climatic differences and the increase in hardwood presence at lower elevations, we first examine the significance of elevation as a co-variate in an ANCOVA. Model results indicate that this factor is not statistically significant in either size class (Figure 2.7). Changes in hardwood share over the study period between initial stand conditions are also not significantly different from each other in either size class (Figure 2.8).

2.4 Discussion

Our study finds no significant evidence to support hypothesized shifts in composition of high elevation forests from *P. rubens* and *A. fraseri* to hardwood species over the last two decades. Our data showing the persistence of *A. fraseri* corroborates results of other studies; the

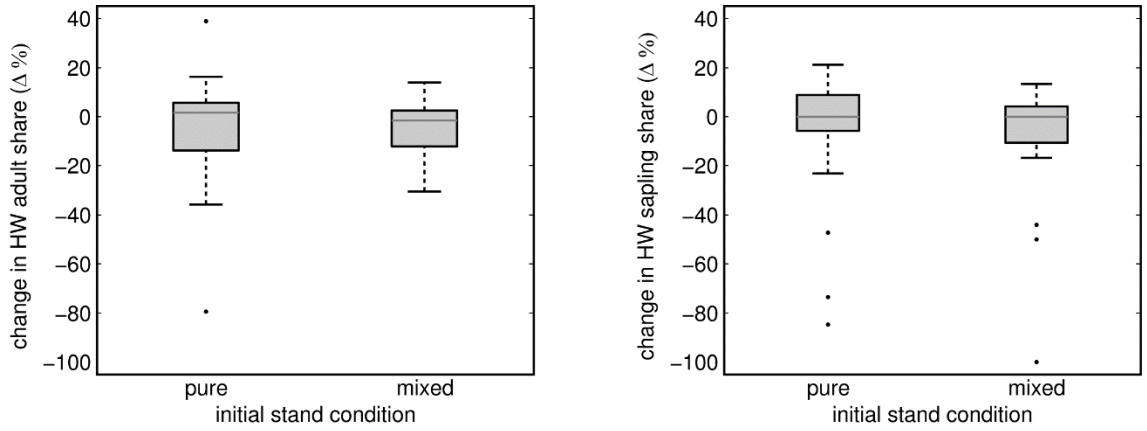

Figure 2.8. Change in hardwood share in overstory BA (left) and sapling density right) from 1990-2010 in 37 long-term *Picea rubens-Abies fraseri* monitoring plots in Great Smoky Mountains National Park by stand composition at the time of establishment in 1990. "Pure" designates plots with overstory composition greater than 65% fir in 1990, while "mixed" indicates those that were less 35% fir. The central mark represents the median value, edges of the box are the 75th and 25th percentiles, whiskers extend to the most extreme values that are not an outlier, outliers are defined as points that fall outside of +/- 1.5 times the interquartile range.

thirty to fifty year recovery of *A. fraseri* canopy has been noted at other locations within the species range (Lusk et al. 2010; McManamay et al. 2011; White et al. 2012).

High elevation *P. rubens-A. fraseri* forests in the southern Appalachians receive much higher nitrogen amounts annually than is typical in related boreal forest communities (Johnson et al. 1991; Nodvin et al. 1995; Gundale et al. 2011). While temperate forests are often considered to be N-limited (Vitousek & Howarth 1991), the montane forests in the GSMNP have been considered N saturated since the late 1990's (Fenn et al. 1998). It is important to note that Weathers et al. (2006) state that their model underestimates deposition rates at the highest elevations, so that actual values may be higher than what we have used for analysis. In addition, though increasing regulation has been put in place on air quality standards in the southeastern US, according to a briefing statement from the National Park Service, substantial decreases in NO_x or NH_4 deposition in the GSMNP have not been observed (personal communication Jim Renfro). Research on nitrogen deposition effects on tree communities in the southeastern US is lacking, but studies have shown that nitrogen deposition levels in the eastern US have exceeded critical loads for long enough to have substantial impacts on herbaceous plant communities in much of the region (Gilliam 2006; Clark et al. 2013) .

The lack of a significant effect of N deposition rates on forest composition changes in the present study are likely driven by three factors. First, it is likely that *A. fraseri* regeneration is being stimulated by nitrogen addition through atmospheric deposition. It has been shown that *A. fraseri* seedlings are able to utilize both NO_3- and NH_4+ for growth (Rothstein & Cregg 2005). Contrary to previous findings about N preferences in shade-tolerant late successional species under acidic soils, Rothstein & Cregg (2005) found that *A. fraseri* seedlings performed better in terms of growth and photosynthetic rate with greater NO_3-, which is the form increased under deposition. It may be that conifer seedling survival and persistence is greater in the presence of atmospheric N additions. In a study on the effects of nitrogen addition on understory tree regeneration in Harvard Forest, Catovsky & Bazzaz (2002) found that the coniferous *Tsuga canadensis* was the only species to show a positive response in seedling survival to nitrogen addition, and this response was significant over many growing seasons.

Secondly, atmospheric N addition may not provide as great a benefit to hardwood trees as previously hypothesized. In a study of long-term N addition effects on 6 species of hardwood trees in the Catskill Mountains (*Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Tsuga*

canadensis, and *Quercus rubra*), no significant effects of 6 years of elevated N application were observed on woody biomass increment or above-ground net primary production for any species though some species showed significant increases in foliar N (Lovett et al. 2013). In addition, in the previously mentioned study on understory tree regeneration in Harvard Forest, nitrogen addition had no significant effects on survivability or growth of understory *B. alleghaniensis*, while *Acer rubrum* and *Acer saccharum* both exhibited nitrogen-induced declines in survival, particularly in early life stages (Catovsky & Bazzaz 2002).

Finally, a greater proportion of N addition could be used by understory herbaceous plants and soil ecosystems than that acquired by woody species. Many of the plots sampled contain abundant understory cover of the *Rubus sp.* and *Dryopteris sp.* which are associated with canopy disturbance in the *P. rubens-A. fraseri* forest (Crandall 1958). Related members of both of these genera have been found to be demonstrably nitrophilic (Falkengren-Grerup 1989; Rodenkirchen 1992; Falkengren-Grerup & Schöttelndreier 2004), so it is possible that these plants are responsible for significant sequestration of N capital into their biomass. A long-term nitrogen addition study in the Catskills found N treatment caused a significant increase in C stock, N stock and C:N ratio in the forest floor, with the largest effect in *Tsuga canadensis* plots, suggesting that excess N may cause accumulations of C in the forest floor in coniferous forests (Lovett et al. 2013).

Because of local weather patterns, the highest elevation plots and those with a northern or western aspect are generally those which have greater nitrogen deposition rates (Lovett & Kinsman 1990). Climate at these sites could be a limitation to hardwood establishment and dominance; important climatic factors at high elevations include shorter growing seasons, colder temperatures, and more ice, snow and wind damage and these effects are more pronounced on northern and western aspects. These climatic limitations may be mitigating benefits to species which have faster growing or nitrogen cycling and favoring stress-tolerant species like *P. rubens* and *A. fraseri* which are adapted to such conditions.

Delcourt & Delcourt (1998) predicted the elimination of southern Appalachian *P. rubens-A. fraseri* forest with a global mean temperature increase of 3 C caused by greenhouse-effect warming. This warming is already underway; Karl et al. (2009) report that during 1970-2008 the mean annual temperature in the southeastern US has increased 0.9 C and mean precipitation has decreased 7.7 percent. Our data show no evidence of elevational range shifts from *P. rubens-*

A. fraseri forest type to hardwood forest type in Great Smoky Mountains National Park. However, potential climate change impacts on the *P. rubens-A. fraseri* forests are not well understood. If the ecotone between forest types is shifting to higher elevations as a result of changes in climate, longer term monitoring and a more thorough investigation incorporating fine-scale climate data and comprehensive examination of forest cover is needed. It may be that in GSMNP's temperate forests, local topography and high soil moisture may buffer regional warming temperatures (Fridley 2009). Recent studies have shown a significant contribution of cloud immersion to *A. fraseri* water relations (Reinhardt & Smith 2008; Berry & Smith 2012; Berry & Smith 2013); cloud cover may be an important mitigating factor with respect to the effect of warming temperatures on *P. rubens-A. fraseri* forests. Additionally, Hagen (2006) reported varying response to increased temperatures among *P. rubens* of differing seed source, so certain populations or genotypes of conifers may exhibit physiological acclimation to changing temperature. Any of these factors, or a combination of them, may explain the lack of forest species shifts with respect to elevation in our study.

Lastly, our analysis finds no significant differences between stands which were mostly fir and those that were predominantly hardwood in 1990. While we might surmise propagule pressure would differ between different species in different stand types, seed size and dispersal mechanisms play an important role in post-disturbance forest plant dispersal and growth (Marks 1974; Grime 2001; Wilfahrt et al. 2014). Time since disturbance (in this case, that associated with *Adelges piceae* infestation) may be an important consideration in tracking successional changes in hardwood forests as understory firs are recruited into the overstory. Because understory dynamics are predictive of future overstory composition (Oliver & Larson 1996) and our data show no increase in the hardwood share of the sapling class, we also predict no significant hardwood increases in the overstory in the short term.

In addition, while we do not see increases in percent composition of hardwood vs. softwood or the number of individual hardwood trees, data suggests changes in proportions of hardwood species. Grime's Universal C-S-R theory predicts that a major disturbance of a community dominated by stress tolerant species will be followed by an increase in ruderal plant species, which will decline as forest succession processes continue. This decline will be driven by increases in competitive and competitive-stress tolerant species (Grime 2001).

In the specific case of the high-elevation forests of the southern Appalachians, the mortality of 90% of mature *A. fraseri*, a stress tolerant-competitor species, caused an abundance of space and resources for colonization. The vegetation recolonization sequence of species abundance through time is much like that described by Marks (1974) in his study of post-disturbance changes in northern hardwood forests. He describes the quick response of *P. pensylvanica* and *B. alleghaniensis* from the seed bank to available resources following canopy disturbance, with. populations of *B. alleghaniensis* stabilizing while after 25 years, populations of *P. pensylvanica* declined dramatically to be replaced with the late successional *Fagus grandifolia*.

We found that *Prunus pensylvanica*, a ruderal species, quickly becomes abundant in the overstory and provides shade for the subsequent establishment of *Acer* species which are generally classed as ruderal competitors (Marks 1974; Grime 2001). *Betula alleghaniensis*, as a competitive strategist, also becomes abundant fairly early and populations stabilize within the forest (Moore et al. 2008). Later increases in overstory abundance in competitive-stress tolerant species, like *Sorbus americana*, *Quercus rubra* and *A. fraseri*, begin to replace trees with more ruderal strategies. See Wonkka et al. (2013) for species classification of life history strategies. However, we note overall declines in *F. grandifolia*, generally thought to be stress tolerant, possibly a result of Beech bark disease which has been responsible for widespread *F. grandifolia* mortality throughout much of the region (Wiggins et al. 2004; McCann & MacDonald 2012).

2.5 Conclusions

To evaluate previous hypotheses of shifts in forest types associated with selective long term stress and disturbance, this study analyzes data from 20 years of forest monitoring in high elevation forests in the Great Smoky Mountains National Park. We find no evidence to suggest shifts in forest composition to greater dominance of hardwood species either from long-term N saturation or climate change as reflected in elevational gradients. Additionally, we find no statistical difference between forests which were mostly fir and those which had a greater hardwood abundance at the time of canopy disturbance in terms of change in hardwood share. Instead data suggests both recruitment of *A. fraseri* into the overstory and trade-offs in hardwood species with different life history strategies.

Acknowledgements

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Chapter 3

Recovery trends and predictions of Fraser fir dynamics in the Southern Appalachian Mountains

Abstract

The southern Appalachian spruce–fir forests are relic forests which exist only in seven montane regions in North Carolina, Tennessee, and Virginia above ca. 1,500 m elevation, and are home to the endemic Fraser fir (*Abies fraseri*). Due to widespread insect-caused mortality from the invasive balsam wooly adelgid (*Adelges piceae*) as well as possible impacts from climate change and atmospheric pollution, the future of Fraser fir populations remains uncertain. Long-term monitoring programs have been established in this forest type since the 1980's, and here we present predictive population models using the inventory data for Fraser fir in Great Smoky Mountains National Park, which contains 74% of extant Fraser fir forests. Using two kinds of population data (understory density counts and overstory census data) we model Fraser fir populations on five different mountaintops as a stage-structured matrix with transition parameters estimated using hierarchical Bayesian inference. At Clingmans Dome, where mature overstory fir has persisted throughout the last two decades, Fraser fir populations are predicted to increase, reaching 3,800 trees ≥ 5cm dbh. We also predict robust Fraser fir populations on Mount LeConte for at least the next several decades. In contrast to these sites, our model predicts that average overstory fir densities on Mount Collins and Mt Guyot will slowly return to the 1990 level by mid-century. Further, our model predicts the fir population to decline at Mount Sterling, which is at the lower bound of the species elevation range. Fraser fir densities are already low at this site, suggesting this population is vulnerable to local extirpation, and we suggest management strategies to address this.

3.1 Introduction

The southern Appalachian spruce-fir forest is a relict ecosystem found in only six mountain-top populations ranging from Mt. Rogers in southwestern Virginia to the Great Smoky Mountains of eastern Tennessee and western North Carolina (Ramseur 1960; Whittaker 1956). Currently occupying only about 26 kha (Smith & Nicholas 2000), the red spruce (*Picea rubens*)-Fraser fir (*Abies fraseri*) forests of the Southern Appalachians are currently listed as one of the most endangered ecosystems in the United States (Christensen et al. 1996; Noss et al. 1995). These forests are noted for their relatively high level of endemic species, especially within the pure fir stands found on the highest peaks (White 1984).

The current geographic distribution of Fraser fir covers about half of what it once did in the late nineteenth century (Dull et al. 1988). Logging and failed regeneration caused by site degradation dramatically reduced the range of Southern Appalachian spruce- fir in the early 1900s (Pyle & Schafale 1988; Pyle 1984). Since the late 1950s, Fraser fir has experienced 67% mortality of adult trees throughout the species' range, with up to 91% mortality in the Great Smoky Mountains National Park (Dull et al. 1988; Eagar 1984). Impacts potentially contributing to this decline are numerous. One well-known factor is depredation from the invasive insect *Adelges piceae,* the balsam wooly adelgid (BWA). The insect feeds on the phloem of adult Fraser fir and causes reduction in water and sap conductance, which generally results in tree mortality in 2-5 years (Hollingsworth & Hain 1991). Additionally, acidic deposition associated with air pollution is high in the montane cloud forests of the southern Appalachians (Cai et al. 2011; Johnson et al. 1991; Nodvin et al. 1995), and has been linked to increased foliar injury and early senescence, reduction in leaf chlorophyll content, decreased cold hardiness, and alterations in soil aluminum and nutrient availability (Borer et al. 2005; Eagar & Adams 1992; Jacobson et al. 1990; McLaughlin et al. 1990; McLaughlin & Wimmer 1999). Alterations to carbon balance and foliar respiration associated with changing climate are another possible reason for reduced forest health (Alexander et al. 1995; Gunderson 2000; Tjoelker et al. 1999). Finally, human use of these areas may impact forest regeneration directly through trampling of seedlings or cutting down saplings, or indirectly through the removal of coarse woody debris or by influencing seed dispersal.

In the face of these relatively rapid changes, the future of Fraser fir populations remains uncertain. The US Forest Service's 1988 regional assessment of spruce fir forests using aerial photography was the last systematic inventory to document the total extent of high elevation forests in the southern Appalachians, but is limited to presence/absence data for this forest type at a single point in time. Several descriptive studies were done prior to the arrival of BWA (Oosting & Billings 1951; Ramseur 1960; Whittaker 1956), and other studies document changes occurring during the infestation's initial outbreak (Busing et al. 1993; Busing et al. 1988; Dull et al. 1988).

Long-term monitoring programs were established during the 1980's throughout the range of Fraser fir. A number of studies have detailed forest dynamics over the past few decades at these sites (Jenkins 2003; Lusk et al. 2010; Mancusi 2004; McManamay et al. 2011; Moore et al.

2008), and generally describe juvenile and understory forests reaching the stem exclusion phase of stand development, indicating recovery from disturbance is underway. In addition, Dale et al. (1991) generated paired leslie matrix models for both Fraser fir and BWA to perform scenario analysis at different elevations. This study concluded that oscillations in BWA and fir populations with a cyclical pattern of mortality and recovery were likely but did not detail the length of this cycle. Additionally, because temperature ranges and amplitude affected the survival and fecundity of BWA, these factors had an indirect, but significant impact on future Fraser fir populations. Finally, some predictive climate envelope modeling has also been performed on Fraser fir based on current species distributions (Potter et al. 2005) and suggests suitable habitat will shrink by 2050 and then expand again by the end of the century. However, there are no predictive population models using the inventory data collected from monitoring efforts. By locating specific populations that are in decline, predictive population models could benefit management and conservation of this endemic species by allowing managers to concentrate their efforts on these key populations.

In this paper, we describe past and current Fraser fir forest structure on five peaks in the Great Smoky Mountains National Park. Additionally, we present the first predictive population models for Fraser fir in the Park: a set of stage-structured matrix models fit using Bayesian methods. We then use these models to generate predictions of Fraser fir stand density in ten year increments until 2050, as well as error estimates around those predictions.

3.2 Methods

3.2.1 Study Area

Fir populations were monitored by the National Park Service in five high-elevation mountaintop sites in the Great Smoky Mountains National Park (GSMNP). These five mountains encompass nearly the entire Fraser fir range in GSMNP: Mount Sterling, Mount Guyot, Mount LeConte, Mount Collins and Clingmans Dome (Figure 3.1). Thirty-seven long-term monitoring plots were established at these sites in 1990 with roughly eight plots on each mountain (exceptions being six plots on Mount Sterling and seven on Mount Guyot). Plots measure 400 m^2 and are situated at different aspects and elevations, ranging from 1,722 m on Mount Sterling to 1,999 m on Mount LeConte.

3.2.2 Data

Forest plots were measured over the summers of 1990 and 2000 by National Park Service (NPS) staff, and 2010 by D. Kaylor and NPS staff. Species and diameter at breast height (dbh) were recorded for all adult trees (dbh > 5 cm) in each plot, which are labeled with a unique identifier. Total counts by species of seedlings (height < 1.37 m) and saplings (height > 1.37 m, dbh < 5 cm) were also recorded within 12 1×1 m subplots and 12 2x2 m subplots, respectively.

3.2.3 Past and Current Population Size Distributions

Data collected in 1990, 2000, and 2010 were used to generate both current live fir basal area as well as past and current size class distributions. Seedlings were approximated as all having a

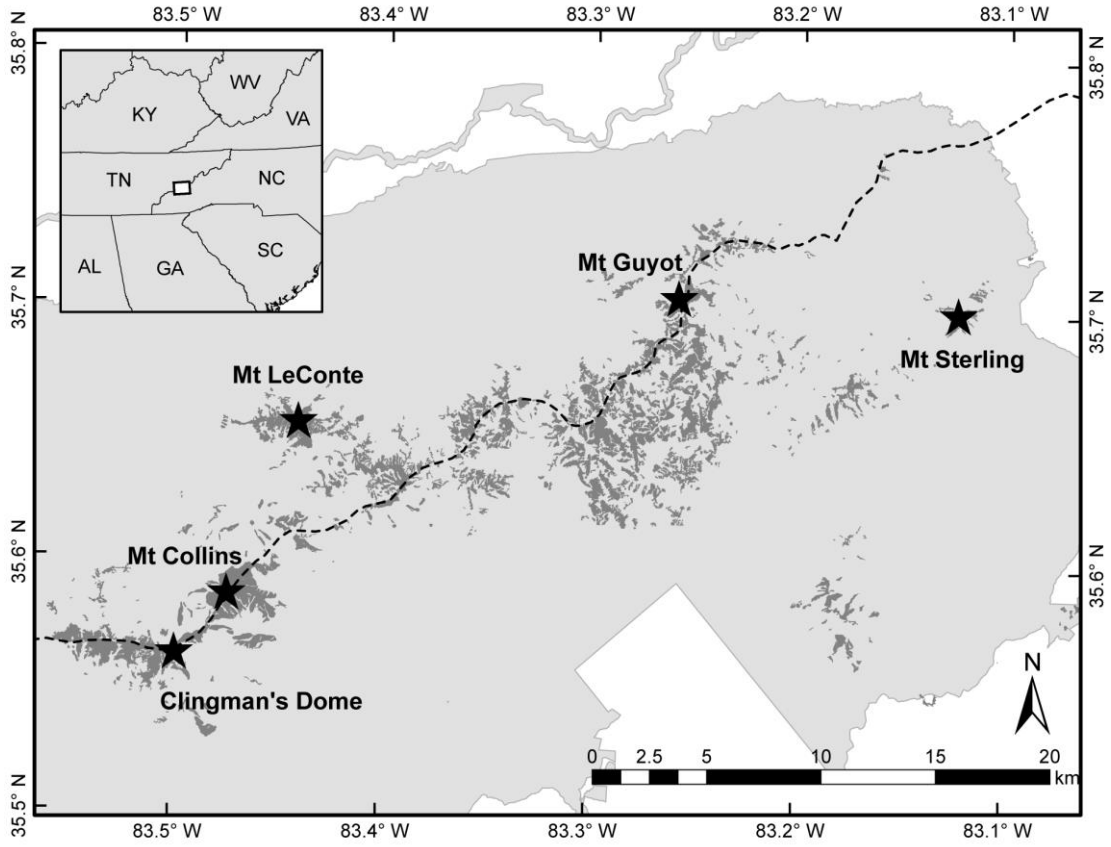

Figure 3.1: Map of study area within Great Smoky Mountains National Park. Light grey shading denotes park boundary. Dark grey shading represents red spruce-Fraser fir forest cover provided as a GIS layer from the National Park Service. Stars denote the five mountains where monitoring plots are located.

size = 0.5 cm (from an estimated range of 0 – 1 cm), and saplings as having a size of 3.0 cm (estimated range of 1 – 5 cm). Then, a kernel density estimator was applied to adult size data to estimate counts of adult trees in 1 cm increments. Error was estimated by means of a leave-one-out (jackknife) cross-validation over the plots for each mountain. Because seedlings are substantially more dense within plots than large overstory trees, data is reported on a log scale.

3.2.4 Population Model

Population growth of Fraser fir on each mountaintop was modeled by a stage-structured matrix with transition parameters estimated using hierarchical Bayesian inference (Figure 3.2). The fir population is divided into four stage classes: seedlings (S), saplings/juveniles (J), non-reproductive adults (A), reproductive adults (R) defined as adult trees with dbh > 15 cm, plus an additional 'stage' for dead stems (D) to account for the fate of all individuals over the study period. Over the two ten-year periods, individuals transitioned between stages. In the case of adult trees, these individual transitions were documented; in the case of saplings and juveniles, these transitions must be inferred from the aggregate count data. These stages, transitions, and recruitment rates define a matrix population model (Caswell 2001; Ellner & Guckenheimer 2006).

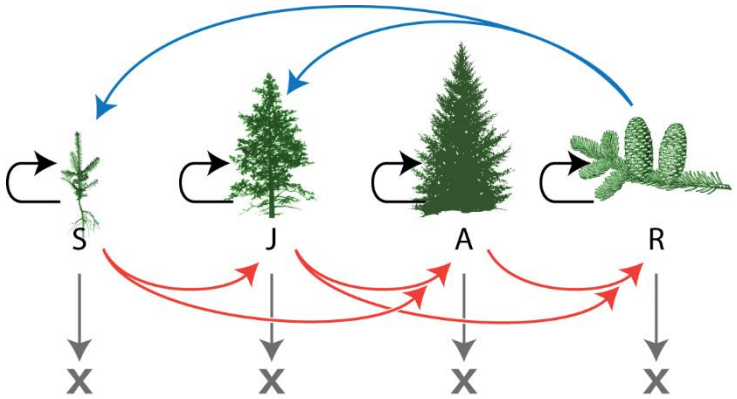

Figure 3.2. Model schematic showing stages for seedlings (S), saplings (juveniles, J), non-reproductive adults (A), and reproductive adults (R). Between 10-year iterations, individuals may remain in their current stage (black arrows), transition to an older stage (red arrows), or die (gray arrows); additionally, reproductive adults may generate new individuals in the seedling or, less frequently, juvenile class (blue arrows).

In the case when all transitions and recruitment events are recorded, those rates can be straightforwardly estimated from observed proportions. However, when only counts are available, those rates are not fully determined and the same data can be observed from different vital rates (Caswell 2001; Wood 1994). When given multiple observations with the goal of determining vital rates over all samples, multiple regression techniques (Lee et al. 1977; Lefkovitch 1965) and iterative methods (Lawless & McLeish 1984; MacRae 1977) are well established. However, these techniques provide point-estimates only, and combining different types of data into the same model is challenging. A Bayesian approach can estimate model parameters using all of the available data. Additionally, it can provide uncertainty estimates around those parameters that can be propagated to functions of those parameters, such as future population estimates (Gross et al. 2002).

Given that individuals may transition from stage to stage between observations, let m_{ij} represent the number of individuals that were in stage j at the beginning of a ten-year period and were then in stage *i* at the end of that period, including the cases where those individuals remain in the same stage (i.e. *i=j*). These values are multinomially distributed (Welton & Ades 2005) with parameters equal to the conditional probability of an individual ending in stage *i* given it started in stage *j*:

$$m_{Sj}, m_{Jj}, m_{Aj}, m_{Rj}, m_{Dj}] \sim \text{Multinomial}(p_{Sj}, p_{Jj}, p_{Aj}, p_{Rj}, p_{Dj})$$

It is these probabilities, p_{ij}, that define the matrix model. They are themselves given an uninformative prior distribution:

$$[p_{Sj}, p_{Jj}, p_{Aj}, p_{Rj}, p_{Dj}] \sim \text{Dirichlet}(1,1,1,1,1)$$

The Dirichlet is the conjugate prior to the multinomial, and ensures that:

$$p_{ij} \in [0,1]$$

$$\sum_i p\_ij \ = 1$$

These probabilities are combined with (unknown) reproductive rates, b_{ij}, into a matrix, **G**, that defines a linear model of population growth:

$$\mathbf{G} = \begin{bmatrix} p_{SS} & 0 & 0 & b_{SR} & 0 \\ p_{JS} & p_{JJ} & 0 & b_{JR} & 0 \\ p_{AS} & p_{AJ} & p_{AA} & 0 & 0 \\ 0 & p_{RJ} & p_{RA} & p_{RR} & 0 \\ p_{DS} & p_{DJ} & p_{DA} & p_{DR} & 1 \end{bmatrix}$$

The 'dead' stage is absorbing; individuals cannot transition into a different stage after dying. Reproductive adults can generate new seedlings and juveniles at rates equal to b_{SR} and b_{JR}, respectively. These reproductive rates must be non-negative but are not constrained in magnitude. Finally, some theoretically possible transitions in the model that are ecologically infeasible, such as seedlings growing into reproductive adults in ten years, are defined to be zero.

Multiplying **G** with a vector representing the number of individuals in a population within each stage at a given time, $\mathbf{v}_t$ generates an estimate of the stage structure at the end of a ten-year period, $\mathbf{v}_{t+1}$:

$$\mathbf{v}_{t+1} = \mathbf{G}\,\mathbf{v}_t + \epsilon$$

where ϵ is a vector of normally-distributed errors such that:

$$\epsilon_i \sim \mathrm{N}(0, \tau_i)$$

$$\tau_i \sim \mathrm{Gamma}(1, 0.1)$$

and where τ_i is a precision for stage *i*, each of which is given a minimally informative prior distribution.

Because individual adult trees were tracked through time, the number of individuals that remain within the non-reproductive adult class (m_{AA}), remain within the reproductive class (m_{RR}), transition to reproductive adults from the non-reproductive class (m_{RA}), or transition from either adult stage to the dead stage (m_{DA}, m_{DR}) are known for each plot. Therefore, the distribution of the associated transition probabilities can be estimated directly from the multinomial distribution. However, distributions for reproductive rates and the transition proportions for seedlings and juveniles must be estimated indirectly from the linear model using the aggregate count data. The use of the Bayesian modeling approach allows these data types to be seamlessly combined to estimate distributions of all probabilities simultaneously.

The total number of individuals in each stage in 1990, 2000, and 2010 were tallied for each plot, as were the number of known transitions. Plots on the same mountain were considered together to estimate shared parameters. Bayesian hierarchical modeling was used to sample from those parameter distributions using the Metropolis-Hastings algorithm (Hastings 1970) as implemented in OpenBUGS (Lunn et al. 2009). The algorithm was allowed to run for 100,000 burn-in iterations in order to converge; samples were taken over 20,000 additional iterations. Convergence was confirmed by scale reduction factors ($\hat{R}$) very near 1 ($|\hat{R} - 1| < 0.01$) for each monitored parameter (Gelman & Rubin 1992). For each of the five sets of parameter distributions sampled, five parallel chains with initial conditions selected from over-dispersed distributions were aggregated for a total of 100,000 post-convergence samples. The OpenBUGS model specification is available as an Appendix.

Transition matrices of the same form as **G** were constructed from each of the 100,000 parameter samples drawn by OpenBUGS for each of the five mountains. Using each of these matrices, estimates of population structure were projected in 10-year increments from the observed stage-structured population totals on each mountain in 1990, 2000, and 2010. This provided likelihood distributions of population structure for each decade until 2050. In addition, by forecasting populations in 1990 and 2000 and comparing them to known counts in 2000 and 2010, the validity of the model was visually evaluated.

3.3 Results

3.3.1 Past and Current Stand Structure

Stands at Clingmans Dome, Mount LeConte and Mount Collins all show recovery or increases in overstory fir over the last twenty years. Currently these stands have the same average density of overstory fir—approximately 2,000 stems per hectare (Table 3.1; Figure 3.3). Fir forest recovery is particularly dramatic at Mount Collins, where overstory fir (>5 cm dbh) more than doubled in the last decade (Figure 4). In terms of live fir basal area, average basal area is highest on Mount LeConte at 27.3 ($m^2 \cdot ha^{-1}$) (Table 3.1).

Fraser fir stands on Clingmans Dome show the most consistency over the last two decades of any of the five peaks sampled (Figure 3). Reproductive adults (>15 cm dbh) have been persistent over the last two decades. The forest structure currently has a fairly even mix of sizes,

Table 3.1. Average Basal area of Fraser fir ≥ 5 cm dbh and overstory density (with standard errors) from 37 long-term monitoring plots on 5 peaks in Great Smoky Mountains National Park re-measured in 2010 and 2011.

Mountain	Elevation Range (m)	Fir BA (SE) ($m^2 \cdot ha^{-1}$)	Fir stems ($n \cdot ha^{-1}$)
Clingmans Dome	1,937 – 1,993	18.4 (2.8)	2100
Mount LeConte	1,892 – 1,999	27.3 (5.7)	2200
Mount Collins	1,821 – 1,887	15.7 (2.9)	2300
Mount Guyot	1,913 – 1,990	13.7 (5.3)	1000
Mount Sterling	1,722 – 1,783	7.5 (2.1)	500

with a number of larger reproductive trees. Consistently high numbers of seedlings are present in all three sampling times. The large number of 5-10 cm dbh trees sampled in 2000 declined by an order of magnitude by 2010, but likely is the result of these trees growing and moving to larger size classes, which is evidenced by an overall increase in the average number of stems per hectare in mature stems between these two years (Figure 3.4).

Forest stands on LeConte, Collins and Guyot show marked ongoing disturbance, but also recovery of overstory Fraser fir. On Mount LeConte a marked decline in seedling density occurred between 1990 and 2000. While there a decline in average density of trees 8-15 cm dbh, this is coupled with an increase in trees of the largest size classes. On Mount Collins, mortality of overstory trees larger than 20 cm dbh occurred between 1990 and 2000. This is followed by recovery, though large trees >30 cm dbh are not currently common as at many of the other sites. On Mount Guyot, the density of overstory trees < 20 cm dbh doubled between 1990 and 2000, however, many of the largest trees on this peak died over the last decade. This trade-off means that the average density of overstory fir has remained relatively constant since 1990 at about 1,000 trees per hectare.

At Mount Sterling sites over the last two decades, we see a decline in seedlings and saplings by an order of magnitude. Though recruitment from the understory nearly doubled the average overstory fir density from 1990 to 2000, this site has the least dense coverage of overstory fir at about 500 trees per hectare. Our data also show very little increase in larger, reproductive adults (> 15 cm dbh) over the monitoring period.

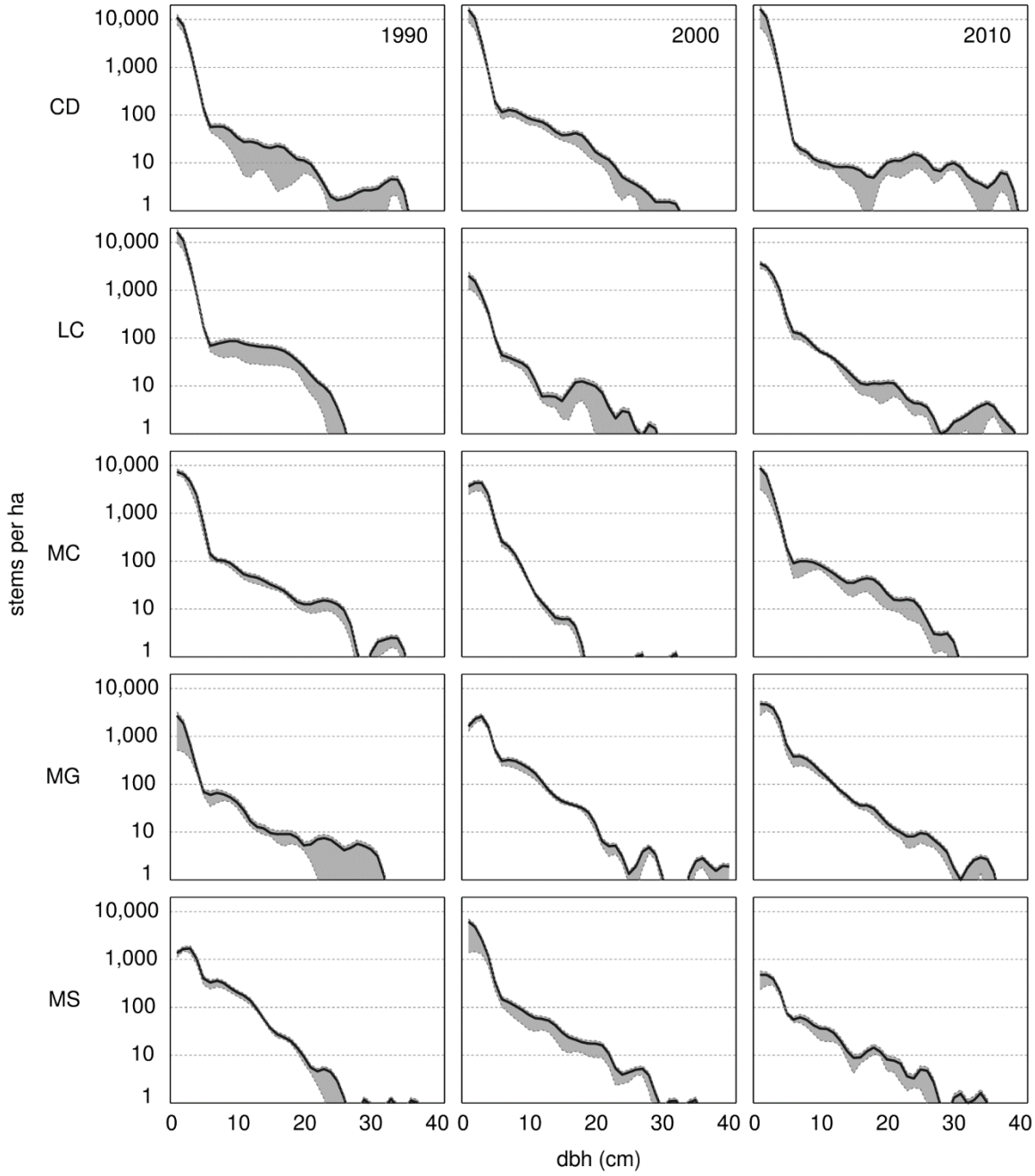

Figure 3.3. Size class histograms for five populations of Fraser fir in Great Smoky Mountains National Park: Clingmans Dome (CD), Mount LeConte (LC), Mount Collins (MC), Mount Guyot (MG), and Mount Sterling (MS). Charts show 1cm DBH size classes in 1990 (right), 2000 (center) and 2010 (left) reported on a log scale. The gray region is the area between the minimum and maximum estimations from jack-knifed cross-validation and represents uncertainty due to sampling; the dark line is the mean for all plots.

3.3.2 Population Model

Though data from all size classes was used to generate the population model, results for overstory and understory size classes are presented separately for ease of interpretation. The majority of observed data points are within the model's 95% prediction intervals.

While stands on Clingmans Dome already show the most complexity as far as live fir size distributions, our population model predicts a further increase in average overstory tree density by 2020. Current live standing overstory Fraser fir density is approximately 2,000 trees per hectare. We predict that this will nearly double by 2020 and then level out, with densities at least as equal to current levels by 2050 (Figure 3.4). For understory size classes, we predict live fir density will stay relatively constant with a slight increase over time indicating continued reproduction (Figure 3.5).

By contrast, model results for Mount LeConte predict that overstory Fraser fir densities will stay at a relatively consistent level at about 2,500 adult trees per hectare (Figure 4). For understory stems, this level will decline by 2020, likely due to stem exclusion of smaller trees. However, as on Clingmans Dome, we predict a slight increase over time indicating continued Fraser fir reproduction (Figure 3.5).

Though stands on Mount Collins increased in overstory fir dramatically over the last decade, this average density is predicted to decline in the next twenty years. By 2040, the predicted average live overstory Fraser fir densities will reach that suggested by applying the model to the 1990 data (Figure 3.4). Understory fir by contrast is expected to remain fairly constant through mid-century (Figure 3.5).

On Mount Guyot, which has had a relatively constant density of adult trees in the overstory at around 1,000 trees per hectare, our model predicts an increase by another 500 overstory trees per hectare by 2020. This increase will be followed by a slow decline, with levels returning to what they were in 1990 by 2050 (Figure 3.4). Understory stems also will continue to decline (Figure 3.5).

Lastly, for Fraser fir populations on Mount Sterling, our model predicts no increase in overstory fir densities, but a steady decline reaching below 1990 levels by 2050 (Figure 3.4). We predict a steady average density of understory stems at around 250 individuals per hectare (Figure 3.5).

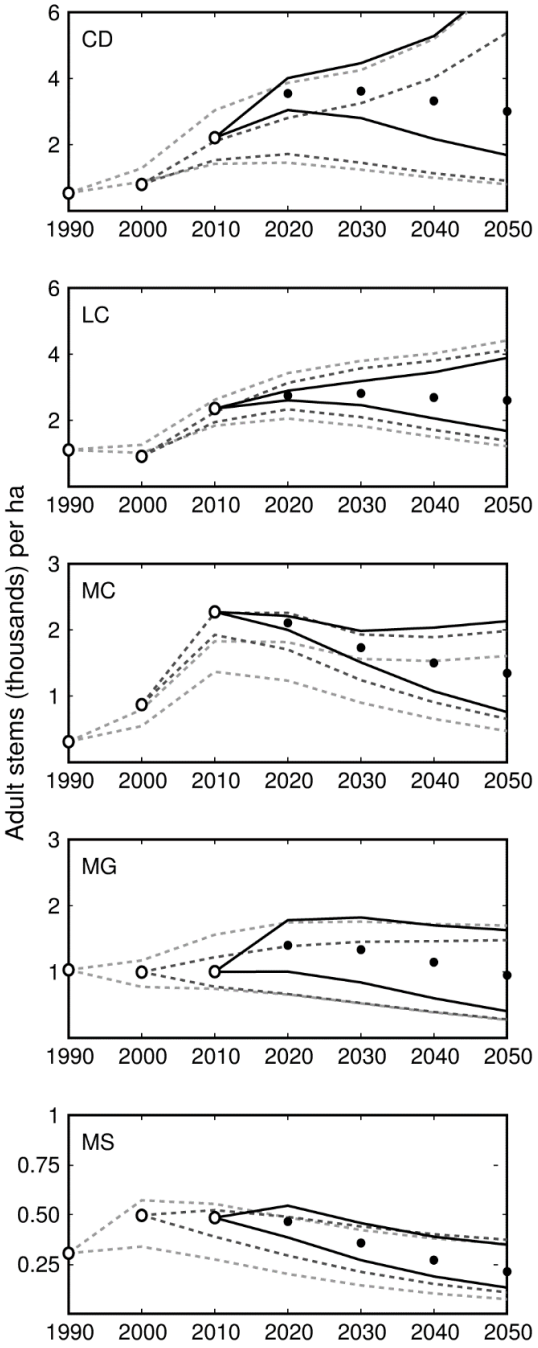

Figure 3.4. Bayesian population model predictions for overstory adult (>5cm dbh) Fraser fir on 5 mountains in Great Smoky Mountains: Clingmans Dome, Mt LeConte, Mt Collins, Mt Guyot and Mt Sterling (top - bottom). Open circles represent measured densities, black dots are projected means. The light gray dotted lines represent the 95% prediction interval of the model as applied to the initial measurements in 1990, dark grey dotted lines are the same bounds as applied to 2000 data, and solid lines the same for 2010 data.

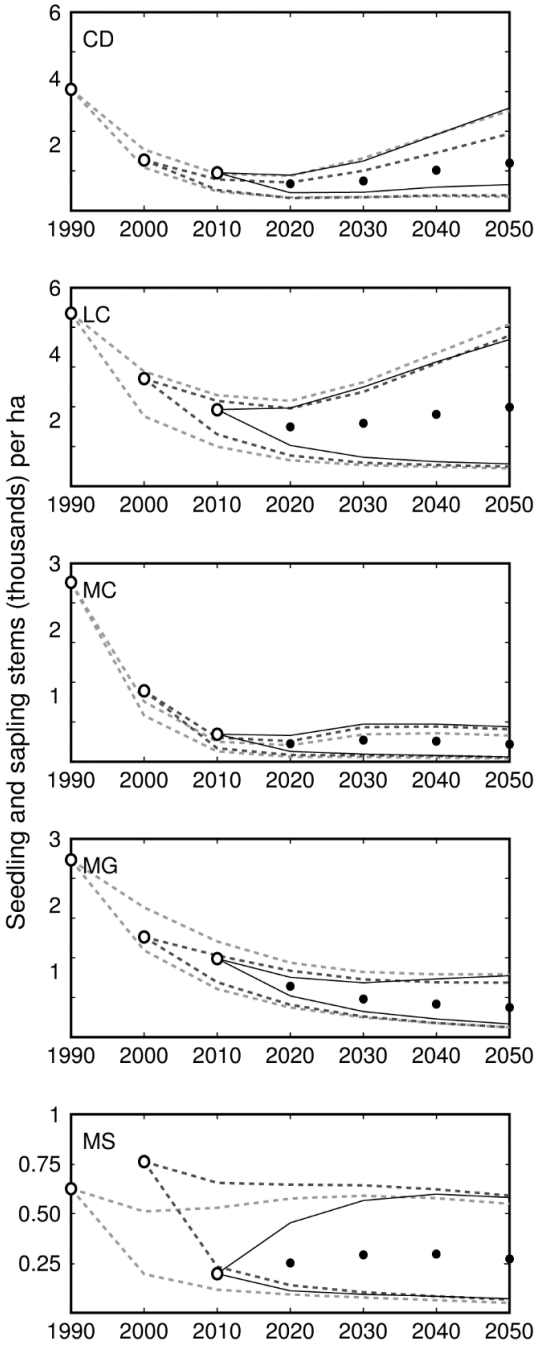

Figure 3.5. Population model predictions for understory seedlings and saplings (<5cm dbh) Fraser fir on 5 mountains in Great Smoky Mountains: Clingmans Dome, Mt LeConte, Mt Collins, Mt Guyot and Mt Sterling (top - bottom). Open circles represent measured densities, black dots are projected means. The light gray dotted lines represent the 95% prediction interval of the model as applied to the initial measurements in 1990, dark grey dotted lines are the same bounds as applied to 2000 data, and solid lines the same for 2010 data.

3.4 Discussion

Pre-adelgid forest census data collected in GSMNP in the 1930's suggest that Fraser fir forests were fairly uniform across the park with an estimated average Fraser fir basal area of 40.7 $m^2 \cdot ha^{-1}$ and an average total basal area of 55.9 $m^2 \cdot ha^{-1}$(Busing et al., 1993). While the average Fraser fir basal areas measured in the present study are considerably lower than these estimates, 3 of the plots measured on Mount LeConte exceeded this number. Average total basal area is 37.9 (Franklin & Kaylor, 2014), also much lower than measured in the 1930's. Additionally, stands at Clingmans Dome, Mount LeConte and Mount Collins all show recovery or increases in overstory fir density over the last twenty years. When considering this most recent inventory data, there is no evidence to support the elimination of Fraser fir as suggested by Smith (1995) and Smith and Nicholas (1998), based on earlier inventories. In addition to recovery in Great Smoky Mountains National Park detailed in this study, Fraser fir forest recovery is also underway on Roan Mountain (White et al. 2012), and in the Black Mountains (Lusk et al. 2010; McManamay et al. 2011).

While overstory forest inventory data are often used to monitor forest recovery, seedling production and the transition rates between life stages are essential components in predicting future forest dynamics. The dramatic declines in seedling density, which are most extreme on Mount LeConte and Mount Sterling over the two decades of monitoring (Figure 3.3), have been previously noted (Mancusi 2004; Smith & Nicholas 2000; Smith 1995). These declines in seedlings may have been caused by increased forest floor insolation (Smith & Nicholas 2000), understory competition (Mancusi 2004; Smith & Nicholas 2000; Smith 1995), or lowered seed production or viability (Fedde 1973a, 1973b; Nicholas 1992). It is only by considering seedling abundance within the context of longer-term population dynamics that this data becomes useful in predicting the restoration and maintenance of a viable fir overstory (Clark et al. 1999). While many individual plots show large reductions in seedling densities over the last two decades, we predict relatively stable overstory fir populations and continued reproduction on Mount LeConte and Clingmans Dome. As has been noted in earlier surveys in Great Smoky Mountains National Park (Jenkins 2003; Smith & Nicholas 2000), Fraser fir regeneration is patchy; this patchiness exhibited in the error estimates in our model.

However, our model does predict a steady decline in the Fraser fir population on Mount Sterling, the lowest elevation mountain in our study. These predictions are consistent with previous estimates of future suitable habitat for Fraser fir using a multi-temporal spatial clustering method of climate envelope modeling (Potter et al. 2005), which showed a pattern of suitable habitat contraction by 2050 and slight expansion by 2100. Additionally, Delcourt and Delcourt (1998) hypothesize that a 3 C increase in mean July temperatures will raise the lower bound of Fraser fir's habitat 480 m in elevation by 2100 CE. The continued decline of Fraser fir on Mount Sterling may be evidence of habitat suitability shifts caused by long-term environmental changes.

The method we present here differs widely from other approaches like niche modeling, which uses current presence-absence data of a species and current and future environmental site parameters to predict the future extent of the species of interest. These models are biased by historical land use change which limits the current geographic coverage of species. Further, the spatial resolution of predictions generated by niche models is limited by the spatial resolution of available environmental data. Additionally, they are not able to incorporate past population dynamics or generate predictions of differing densities, which is a strength of the approach we have used.

Although matrix-models often rely on eigenvalue analysis to determine the eventual fate of the population (Caswell 2001; Ellner & Guckenheimer 2006), the long-term dynamics of the Fraser fir forests in the Smoky Mountains are complex and deeply uncertain. Simple linear models such as the one constructed here cannot generate long-term predictions. Therefore our analysis focuses on the relatively short-term transient dynamics of these populations that is enabled by using the distribution-generating tools of Bayesian methods.

Additionally, the predictive population model we present here assumes no changes will occur in current and chronic stress factors. Because the population data and transition rates on each mountain incorporate individual tree response to multiple environmental parameters (acidic deposition, climate, BWA induced mortality, and others), these are implied in the model and are a source of variability/uncertainty. If, however, these factors change in the future, for instance emissions standards were to decrease the rates of acid deposition well below what these forests have experienced over the last two decades, then our model cannot anticipate or account for the effects this would have on future population dynamics. Further, the model

assumes that the population will not change in its response to ongoing stresses. However, the gene pool may undergo future changes due to selective pressure and/or limited and isolated populations.

The comparison of model predictions of populations in 1990 and 2000 and known counts in 2000 and 2010 provides a visual estimate of model validity. Overall, our model accurately predicts observed data within a 95% prediction interval of the models applied to the 1990 data, with notable exceptions being the 2010 overstory fir density for Mount Collins (Figure 3.4) and the 2000 understory density on Mount Sterling. For Mount Collins, this is likely due to the ongoing overstory mortality between 1990 and 2000 and release of smaller size classes into the overstory (Figure 3.3). Alternatively, it may be that fir populations at Mount Collins are too unstable to model using our approach, or that there are differing population trajectories occurring across this site. However, when 95% prediction intervals are applied to the 2000 data, we clearly see that observed data are on the upper bound of our predicted intervals for both 2000 and 2010. For the Mount Sterling understory, this unexpected spike in the seedling and sapling size class is caused by seedling increases in a single plot. Such spikes in seedling densities are not uncommon following canopy removal, but are often followed by self-thinning as our data demonstrates. Additionally, observed seedling densities at Mount Sterling are currently within the 95% prediction intervals so we believe our model predictions to be accurate.

Two important factors influencing the future of Fraser fir are the severity and timing of future BWA-induced mortality. Frequent and severe mortality events would cause a dramatic departure of this forest type from pre-BWA conditions, while infrequent or milder-mortality events may yield a forest that is quite similar to pre-BWA forests with stable populations of Fraser fir. The emergence of a two aged forest with cyclical BWA outbreaks and overstory fir mortality followed by a regeneration period has been hypothesized (Dale et al., 1991; Eagar, 1984; Mancusi, 2004; Smith & Nicholas, 1998, 2000). We do not yet see evidence of this pattern in these long-term monitoring plots across mountains, which suggests a patchy forest structure that has also been noted in the Black Mountains (McManamay et al., 2011). Forests on Mount Sterling experienced widespread fir death at the summit in 1970–1972, on Mount Guyot in 1980–1982, Mount LeConte in 1982–1984, Mount Collins in 1985–1987, and Clingmans Dome in 1990–1992 (Smith & Nicholas, 2000). The generation time of Fraser fir is roughly 15 years from

seedling to the onset of reproductive maturity (Beck 1990) and even the most recently infested site surpasses this period. Trees greater than 4 cm dbh are susceptible to BWA-induced mortality (Eager 1984), which is sooner than the onset of reproduction.

Another severe wave of overstory fir mortality has not yet swept through; the more time passes before BWA returns, the more time this recovering forest has to return to pre-BWA conditions. We did note the presence of BWA on Mount Sterling while taking field measurements. This may indicate that lower elevations where annual temperatures have a smaller range provide a refugia for the insects, which could contribute to the observed decline in fir density at these sites. Or it may mean that another wave of fir mortality is immanent and beginning again at the site of initial infestation.

While the exact timing of future mortality events is unknown, forest structural complexity may provide some resilience to large infrequent disturbances. Stands where a number of large trees persisted through the infestation, like those on Clingmans Dome, may recover more quickly due to the presence of reproductive trees. Other stands with very little overstory persistence are limited by the survival and maturation of trees present in the understory at initial disturbance. This creates a mosaic-like structure of stands in different stages of regeneration, which has been previously noted (Jenkins, 2003; Smith & Nicholas, 2000; McManamay et al. 2011). Because BWA feeds on mature fir and a contiguous, dense overstory of large, mature fir no longer exists, this structural complexity may provide some resilience to future BWA mortality.

When comparing projected future populations between mountains, clear differences between them emerge. While proximal causes for these differences in outcomes are likely the aforementioned differences in forest structure, there are a number of possible reasons for the persistence of mature trees and the differences in regeneration and mortality rates at different sites. Genetic differences between populations in response to environmental stresses are likely. Individual trees can show a tremendous ability to acclimate to a changing environment, with the magnitude and variability of this response dependent upon species (Larigauderie & Körner 1995; Tjoelker et al. 1999), provenance (Bigras 2000; Gunderson 2000), elevation (Ledig & Fryer 1972), and other factors. In a study of red spruce (a species co-dominant with Fraser fir) acclimation and adaptation to elevated temperatures (Hagen 2006), seedlings grown from seeds collected at one of 4 sites in the GSMNP showed a significantly different response to an increase

in growth temperature, suggesting that individuals capable of thriving under predicted temperatures may exist within local populations. The longevity, vigor and fecundity of trees are determined, at least in some part, by tree physiological parameters like photosynthetic rates, water use efficiency, and the size of nonstructural carbohydrate pools which likely differ between trees in different locations. In addition, environmental factors like temperature, precipitation, and soil chemistry differ across elevations and aspects. The importance of temperature on this system is particularly noted in a scenario analysis of Fraser fir and BWA persistence at different elevations; larger annual temperature ranges increased the longevity of Fraser fir and decreased the spread of BWA, particularly at higher elevations (Dale et al. 1991). Additionally, recent work has highlighted the importance of cloud water and cloud immersion on Fraser fir physiology (Berry & Smith 2012, 2013; Reinhardt & Smith 2008). It is possible that cloud immersion differs across the study area and may account for some of the variation between predicted populations. It is clear that an understanding of the important environmental factors that affect individual tree physiology is needed before long-term predictions of population dynamics can be made.

Our findings have a number of implications for forest management. A number of insecticides are effective in managing BWA outbreaks, but they all must be applied from within the stand to the bole of the tree to the point of saturation (Eager 1984). Because Fraser fir populations are remote and have limited accessibility, saving large numbers of trees this way is infeasible and costly in terms of cost of chemicals and man-hours required for application. Our data suggests that protection of a subset of reproductive overstory adults could ensure continued fir reproduction through future mortality events and speed recovery. Additionally, our model predicts further decline of fir populations at Mount Collins, Mount Guyot, and Mount Sterling and managing for the survival of fir seedlings and saplings may improve future forest densities. Because these sites are all hiking and camping destinations, limitation of recreational impacts may prove beneficial. Firewood collections have been curtailed by NPS at backcountry shelters at Mount LeConte and Mount Collins due to removal of fir saplings (pers communication, Kris Johnson). Additional viable options are the removal of competitive species in the understory such as *Rubus canadensis*, which has been shown to be negatively correlated with Fraser fir seedling densities (Pauley 1989), and planting Fraser fir seedlings at these sites with predicted fir population declines.

3.5 Conclusions

We present the first predictive model for Fraser fir populations in the Great Smoky Mountains National park. We predict robust recovery of select Fraser fir populations for at least the next several decades, as well as continued decline for populations on a number of mountains, notably those at the lowest elevations. Our data suggest forest structural complexity may provide some resilience to large infrequent disturbances like BWA infestation. Stands where a number of large trees persisted through the infestation may recover more quickly due to the presence of reproductive trees. This suggests management strategies that protect a selection of robust and reproductively mature individuals will improve recovery of Fraser fir populations through further mortality events. Further, our findings highlight vulnerable populations which would benefit from limiting human impacts on successful reproduction and recruitment, and may also be appropriate sites for Fraser fir plantings.

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Appendix: BUGS Listing

```
model {

# get survival and transition rates of adults from Panel Data
# sumA[i] and sumR[i] are the same as A0[i] and R0[i], except that
# samples with A0[i]==0 or R0[i]==0 are removed since those are
# not allowed as parameters to dmulti or dbinom
for(i in 1:NUM_ADULT_SAMP){
    sumA[i] <- sum(A2ARD[i,1:3]);
    A2ARD[i,1:3] ~ dmulti(Pa[1:3], sumA[i])
}

for(i in 1:NUM_REPROD_SAMP) {
    R2R[i] ~ dbin(Prr, sumR[i])
}

# get other transition probabilities from aggregate data
for(i in 1:NUM_SAMPLES) {
    # Define the transition model
    S1_mu[i] <- Pss*S0[i] + Bsr*R0[i]
    J1_mu[i] <- Pjj*J0[i] + Pjs*S0[i] + Bjr*R0[i]
    A1_mu[i] <- Paa*A0[i] + Paj*J0[i] + Pas*S0[i]
    R1_mu[i] <- Prr*R0[i] + Pra*A0[i] + Prj*J0[i]

    # Same as putting a noise term on the above equations
    S1[i] ~ dnorm(S1_mu[i], tau_S)
    J1[i] ~ dnorm(J1_mu[i], tau_J)
    A1[i] ~ dnorm(A1_mu[i], tau_A)
    R1[i] ~ dnorm(R1_mu[i], tau_R)
}

# Uninformative prior on precision of normal distribution
tau_S ~ dgamma(1, 0.1)
tau_J ~ dgamma(1, 0.1)
tau_A ~ dgamma(1, 0.1)
tau_R ~ dgamma(1, 0.1)

# Probabilties of moving from Seedlngs
Ps[1:4] ~ ddirch(alpha4[])
Pss <- Ps[1]
Pjs <- Ps[2]
Pas <- Ps[3]

# Probabilties of moving from Juveniles
Pj[1:4] ~ ddirch(alpha4[])
```

```
Pjj <- Pj[1]
Paj <- Pj[2]
Prj <- Pj[3]
# Probabilties of moving from Adults
Pa[1:3] ~ ddirch(alpha3[])
Paa <- Pa[1]
Pra <- Pa[2]

# Probability of staying in Reproduct Adult
# This reduces to Binomial from Multinomal since only two options
# and so has a beta distribution.
Prr ~ dbeta(1,1)

# Uninformative Prior on Reproductive rates
# But constrain Bjr to be somewhat realistic given
# seedling recruitment and survival rates
Bsr ~ dgamma(1,0.1)
Bjr ~ dgamma(mu_pjr,0.1)
mu_pjr <- Bsr*Pjs/Pss /10

#Construct transition Matrix
G[1,1] <- Pss; G[1,2] <- 0;   G[1,3] <- 0;   G[1,4] <- Bsr
G[2,1] <- Pjs; G[2,2] <- Pjj; G[2,3] <- 0;   G[2,4] <- Bjr
G[3,1] <- Pas; G[3,2] <- Paj; G[3,3] <- Paa; G[3,4] <- 0
G[4,1] <- 0;   G[4,2] <- Prj; G[4,3] <- Pra; G[4,4] <- Prr

# Calculuate Eigenvalue for ease of monitoring
# Eigenvalues are unused in analyses.
y[1:4] <- eigen.vals(G[,])
z <- ranked(y[1:4],4)

}
```

Chapter 4

Ecophysiology of Adult Fraser fir (*Abies fraseri*) in High-Elevation Southern Appalachian Cloud Forests

Abstract

The high-elevation forests in the southern Appalachians are dominated by the endemic Fraser fir (*Abies fraseri*) which is under considerable stress due to the depredations of the balsam wooly adelgid (*Adelges piceae*), indirect and direct effects of air pollution, and shifts in climate. Identification of healthy trees would aid land managers in selecting targets for future conservation and restoration efforts. We measured diameter growth, A_{max}, photosynthetic WUE, root and stem NSC pools, SLA, and needle pigment content in 218 adult Fraser fir over 5 mountains in Great Smoky Mountains National Park to identify healthy trees. We also asked how much variation in these measurements can be attributed to plot-scale environmental factors and determined the direction and strength of these relationships with fir physiology. We found metrics associated with carbon gain, storage and growth are largely uncorrelated, and suggest conservation targets be selected to maximize diversity. A_{max} rates were generally low, with highest rates found in trees at the highest elevations and steepest slopes. We find trees at Clingmans Dome have significantly higher A_{max} rates and photosynthetic water use efficiency than those on other mountains, which may suggest greater stress resistance in these trees. NSC pools however, are consistent with those found in mature trees of other species and suggests the capacity for resistance of future stress events, particularly at the highest elevations where photosynthetic rates are the highest. Both WUE and leaf architecture were affected by max July temperature, which indicates future climate change will impact the foliar physiology of this species.

4.1 Introduction

Fraser fir (*Abies fraseri*) is a species endemic to the southern Appalachian mountains and restricted to six island-like populations at high elevations over 1300 m in eastern Tennessee, western North Carolina, and southern Virginia (Beck 1990). A relict of the boreal forest, Fraser fir is adapted to the unique habitat of the high-elevation temperate cloud forests. These forests have a cool climate with a mean annual temperature of 6 C and abundant annual precipitation ranging from 1500-2500 mm $\cdot$ yr^{-1} (Shanks 1954), of which about half is from cloud water deposition (Reinhardt and Smith 2008).

Fraser fir is currently under considerable pressure from many factors. Direct and indirect effects of the balsam woolly adelgid (*Adelges piceae* Ratz.) (BWA) caused widespread overstory mortality during the latter part of the 20th century (Eagar 1984; Dull et al. 1988; Hollingsworth and Hain 1991; Smith and Nicholas 2000). BWA causes alterations to fir xylem anatomy which generally results in hydraulic failure within a few years. High levels of acidic deposition (Eagar and Adams 1992) and high aluminum / low calcium soil concentrations (McLaughlin et al. 1990; McLaughlin and Wimmer 1999; Borer et al. 2005) are also potential contributing factors to decline in the high elevation forest. Acidic deposition results in lowered soil nutrient availability and also causes nutrient leaching from needles and early needle senescence, all of which can reduce needle pigment content and biochemical capacity for carbon fixation. Increased soil aluminum can reduce plant calcium, which is needed for membrane stability and cell signaling. Aluminum can also reduce root growth and increase root turnover rate, resulting in lowered nutrient and water uptake.

Additionally, because Fraser fir occupies a confining temperature niche, climate warming may also be negatively impacting the species. Delcourt and Delcourt (1998) predicted that a 3 C increase in the mean July temperature would raise climatically-limited ecosystems about 480 m in elevation, resulting in the loss of Fraser fir forests. Data from the National Climatic Data Center shows that the average growing season temperature on Mount Mitchell has increased by 2 C since 1996 (McNulty et al. 2014). Temperature determines the relative activity of RuBisCO in carbon fixation, and is a key factor in leaf to air vapor pressure deficit which directly impacts transpiration rates and thus photosynthetic water costs. Additionally high temperatures can result in damages to photosynthetic enzymes and increases of carbon losses to maintenance respiration.

Most studies evaluating Fraser fir decline in the southern Appalachians have focused on population biology, emphasizing long-term changes in tree mortality, recruitment, age-class distribution and community structure (Busing et al. 1988; Dale et al. 1991; Smith and Nicholas 1998; Smith and Nicholas 2000; Mancusi 2004; Moore et al. 2008). Very few studies have evaluated the ecophysiology of this species in natural stands (Johnson and Smith 2005; Reinhardt and Smith 2008; Reinhardt et al. 2009; Berry and Smith 2013), and we know of none that are performed using mature adult trees.

Firs are common throughout the coniferous boreal forest and perform a significant portion of long-term carbon fixation and storage in this forest type, which is responsible for 32% of the global carbon sink (Pan et al. 2011). Fraser fir, at the southern extent of the spruce-fir forest type, live in a range of current environments that may reflect future warming in the northern boreal forest (Karl et al. 2009). An understanding about the local effects of climate and soil nutrients on carbon fixation may therefore be useful to predicting global effects of climate change and help parameterize global carbon models.

Finally, while an understanding of environmental factors influencing fir carbon dynamics and mortality is necessary for predicting future effects, there is also a need to identify individuals that are more tolerant of multiple stresses to act as a source of genetic material for future restoration. Since populations of Fraser fir are fairly isolated from one another on several mountain peaks, some genetic variation would be expected to arise from genetic drift and varying environmental selection pressure. An open question for land managers is how to select target individuals for conservation and management. Because the bulk of spruce-fir forests in the southern Appalachians is on federally managed public lands (White 1984; Dull et al. 1988), a main goal of ecophysiological study of Fraser fir should be to determine healthiest individuals for future conservation efforts like saving genetic material for replanting, or through focused management like the application of insecticides to more vigorous trees.

There are multiple physiological parameters that may reflect tree health and vigor. Fast growth has classically been one of the hallmarks of a healthy forest, but recent work suggests fast growing trees may be less able to withstand chronic stress (McNulty et al. 2014). Foliar measures like maximum photosynthetic rate (A_{max}), and the associated photosynthetic water use efficiency (WUE) are better metrics of the amount of carbon fixation possible under current conditions. Specific Leaf Area (SLA) and pigment content are measures of plant investment of carbon to light-intercepting mechanics, which is also related to plant water loss, leaf longevity, and plant secondary metabolites (Wright et al. 2004; Reich et al. 2007) as well as indicators of plant nutrient status. Finally, reserves of total non-structural carbohydrates (NSCs) may provide the ability to persist through stress events (Niinemets 2010). Studies in the southwestern US have proposed the carbon starvation hypothesis, which explains individual tree mortality in terms of the inability to capture carbon to cover energetic demands especially

under drought conditions (McDowell & Sevanto 2010; Adams et al. 2009). Small sized NSC pools in Fraser fir trees may implicate this mechanism as an important driver in fir decline.

We hypothesize that trees with higher resource investment in photosynthetic pigments would have higher maximum photosynthetic rates. Further, trees which have a greater maximum carbon fixation rate would exhibit greater biomass production and larger nonstructural carbohydrate storage pools. In total, we hypothesize that these physiological measures are indicative of tree vigor, which contributes to survival of the combination of episodic climate variability and chronic stresses. Because these parameters are interdependent (Pollardy 2007), it may be possible to simplify these key physiological parameters into a few dimensions representing underlying factors of vigor, which may be used as a "health score" for selecting individual conservation targets.

Although individuals in a stand may exhibit differences due to genetics or differences in microsite, environmental variables measurable at the stand level may have an influence on growth and physiology. Elevation is expected to influence foliar physiology through changes in specific leaf area. Maximum July temperature is expected to impact photosynthetic water use efficiency, with higher summer temperatures resulting in decreased water use efficiency due to higher transpiration cost. Nonstructural carbohydrate pools may also be impacted by higher summer temperatures as more energy is used for maintenance respiration and growth. Acid deposition levels are expected to decrease leaf photosynthetic pigment amounts which would result in lower maximum photosynthetic rates and lower NSC pools.

In this paper we quantify physiological measures associated with carbon gain and storage in adult trees in a threatened high-elevation cloud forest. We ask if these metrics can be simplified into a few dimensions to form a "tree health" score to find particularly vigorous trees. Then we ask how much variation in the physiological parameters of diameter growth, A_{max}, WUE, root and stem NSC, SLA, and needle pigment content in adult Fraser fir can be explained by plot-scale environmental variables (specifically: elevation, aspect, slope percent, mean yearly temperature, max summer temperature, degree days, available water supply, annual acidic deposition amounts, soil pH, soil Al, and soil nutrient levels), and we determine the direction and strength of these relationships. We view key physiological parameters in terms of temperature gradients for insight into the role of climate change on Fraser fir tree carbon dynamics. Lastly, we compare physiological measurements between mountains to

identify populations which may possess genetic resources relevant to survival of multiple chronic stresses.

4.2 Methods

4.2.1 Study Area

The study was performed in Great Smoky Mountains National Park (GSMNP) over five peaks, which represent nearly the entire Fraser fir range in GSMNP: Mount Sterling, Mount Guyot, Mount LeConte, Mount Collins and Clingmans Dome. None of the areas have been previously logged or burned (Pyle 1984; Pyle and Schafale 1988). Thirty seven research plots measuring 200 m^2 were spread over these five peaks, ranging in elevation from 1,722m on Mount Sterling to 1,999m on Mount LeConte.

4.2.2 Physiological Measurements

Six co-dominant trees in each plot were selected for physiological study. Where possible, the six trees selected were those cored and aged in a previous study (Mancusi 2004). In the event that a given tree died in the previous decade, an alternate co-dominant tree of a corresponding size to the others sampled was randomly selected. When there were not 6 co-dominant trees within a plot, as many were found, saplings and small adults were not sampled so as not to skew results from ontological differences. Trees ranged in size from 6.2 to 34.2 cm dbh, and, according to size-age curves produced by Mancusi (2004), all trees were greater than 22 years of age. No BWA were noted on any of the sampled trees during data collection. Shoot level gas exchange measurements were not made on trees on Mount Guyot; tissue samples were, however, collected from trees in all plots for biochemical analysis.

Diameter growth was obtained by using dbh measurements obtained from National Park Service made in 2000 and those collected in 2010 as detailed in Chapter 3. In the few cases where growth rate could not be calculated because trees were smaller than 5 cm dbh in 2000 at the time of data collection, the average growth rate of the plot was used as an approximate growth. This is a common method of data imputation for missing data (Manley 2004).

At the end of the growing season in 2011, wood and root samples were taken from each tree. Increment cores were taken from a height of 1m, approximately where the trunk

buttressing ends, avoiding the compression wood formed on the up-slope side, and the borer was not greased to avoid future complications with chemical analysis. Roots were collected, verifying that they came from the target tree; root samples were a mixture of fine and lateral root tissue (< 1 mm diameter when dried). All samples were placed on ice and transported to the lab, where they were dried at 100 C for 24 hours then at 70 C for 72 hours and ground using a mechanical grinder to pass through a 2 mm sieve. Sugars were extracted from tissue samples with ethanol and then then measured colorimetrically using phenol-sulfuric acid. The remaining starch in the residue was then solubilized by sodium hydroxide, hydrolyzed to glucose by an enzyme mixture of α-amylase and amyloglucosidase, and measured colorimetrically using a peroxidase-glucose oxidase-o-dianisidine solution (Chow and Landhäusser 2004).

Measurements of maximum photosynthetic rates and transpiration rates were made during the summer of 2012 using an infrared gas analyzer (IRGA) LI-6400 Portable Photosynthesis System (LICOR, U.S.A.) with a conifer chamber attached. To reduce variations between plots, gas exchange measurement collections were taken between 9:00 am and 12:30 am (based on findings from Reinhardt et al. 2009), from from fully expanded non-shaded shoots from mid-canopy over a two month period during July and August. No plot experienced drought conditions during this period. Shoots were clipped from the canopy using pole pruners and measurements were made within six minutes of incision to prevent stomatal closure and concurrent declines in photosynthetic rates. Meng and Arp (1993) investigated photosynthetic gas exchange in red spruce twigs before and after detachment from the parent tree and found that A_{net} and stomatal conductance did not decline significantly within that time; this was also verified in the field. No collections were taken during rain, and all shoots were blotted to absorb excess water prior to measurements. Since the high elevation forests of the smoky mountains are often cloud immersed with high humidity, air intake was routed through 1 m of coiled cold-trap followed by a desiccant chamber in order to stabilize humidity and vapor pressure deficit within the IRGA measurement chamber to standardize gas exchange measurements. The air intake tube was placed at least 1m from the ground to minimize fluctuations in CO2 from ground level respiration. Total photosynthetic active radiation (PAR) was provided by a flourometer at 700 $\mu mols \cdot m^{-2} \cdot s^{-1}$ at 10% blue. This light level was selected based on light response curves published by Reinhart (2009). Chamber conditions were set as close to ambient

as possible, with a block temperature of 20 C. Though every effort was made to standardize gas exchange measurements, variation between plots may still be confounded by preceding weather conditions at each plot and time of year, which are unavoidable due to the nature of *in situ* measurements over a wide geographic region.

Photosynthetic Water Use Efficiency (WUE), the amount of carbon gain per unit water loss, was calculated from measured A_{max} and E values.

Measured shoots were then placed in plastic bags in a cooler and taken back to the lab to measure leaf area in order to standardize gas exchange measurements. Needles were stripped from the shoot and placed on a flatbed scanner; total leaf area was calculated from the resulting images using MIMSI, a MATLAB (2014A, MathWorks, Inc.) tool developed for this purpose. The program is a graphical user interface created in MATLAB to load scans of needles and cluster the spectral signal of the image using k-means clustering. A user then is able to divide clusters into those that correspond with the needles and those that correspond with the background. The interface allows the user to tweak the separation using a variety of automated image morphological operations, such as expanding or contracting around all objects or filling gaps, and also by hand-editing the object mask. Total needle area was calculated by the number of pixels designated as needle standardized by the resolution of the scanned image.

Needles were freeze dried for 72 hours to obtain dry weight. Approximately 100 mg of needle from each shoot was analyzed for pigment content. Pigments were extracted using 100% methanol and the quantity of Chlorophyll A and B and total carotenoids in each sample determined from light absorbance in a spectrophotometer (ThermoScientific, Biomate3) at wavelengths of 470, 666, and 653nm using the formulas presented by Lichtenthaler and Wellburn (1983) standardized by needle weight.

4.2.3 Plot-Scale Environmental Data

We used ArcMap (10.1, ESRI) to generate plot elevation, aspect, and slope percent from GPS coordinates taken at plot center. Plot level temperature data for GSMNP was obtained from the model produced by Fridley (2009). We use degree days, maximum July temperature and average annual temperature for each of the sample plots in our analysis.

Down-scaled precipitation data for GSMNP is not available. We use available water supply (AWS), which is the total volume of water (in centimeters) that should be available to plants when the soil, inclusive of rock fragments, is at field capacity. Plot level AWS was obtained from the USDA Natural Resources Conservation Service Web Soil Survey Database.

Annual N and S deposition estimates were obtained using the acid deposition model produced by Weathers et al. (2006). This is a general linear model relating deposition index to landscape variables measured in the field in 2000 using 378 point measurements and corresponding landscape variables throughout GSMNP and validated using field data. Estimates for annual nitrogen and annual sulfur deposition for each plot were obtained using this model and summed to form a total annual amount of acid deposition at the plot scale.

To measure soil nutrient availability and soil aluminum content, three soil samples were randomly collected from each plot. Though Cai et al. (2011) showed significant differences in soil chemistry between the A horizon and the B horizon at nearby Nolan Divide, tree roots grow through both layers in response to available nutrients and so both layers were mixed into a single sample. Samples were procured from depth of no greater than 25 cm using a polycarbonate plastic hand trowel, and the three samples were combined into a composite sample for each plot. All soil samples were air dried at room temperature and sent to the Clemson University Agricultural Service Laboratory for analysis of soil nutrient levels. Though we report summary statistics for soil nutrients in Table 4.1, to simplify analysis, we used a subset of these measurements that we considered to be biologically relevant to our system: pH, P, K, Ca, and Al levels and Cation Exchange Capacity (CEC).

4.2.4 Statistical Methods

Needle carotenoids, total chlorophylls, SLA, A_{max}, WUE, and NSCs of roots and stem were considered as physiological metrics of tree health to be reduced into a health score using principle components analysis. Covariances were calculated between each pair of z-score normalized metrics, thereby retaining data for Mt. Guyot in comparisons that did not include A_{max} or WUE, which were not available for those sites. Principle components were calculated as the eigenvectors of the pair-wise covariance matrix.

Because environmental predictors are plot-scale, the upper limit to the amount of variation in each physiological parameter explainable by any set of plot-scale environmental predictors is

simply the amount explainable by the plot label. For each physiological parameter, a one-way ANOVA was performed to partition variation in physiological metrics between that which is explainable by plot and that which is due to the combined effects of tree history, genetics, micro-environmental effects, and measurement error.

Plot-scale means of each physiological parameter were calculated for each site, and regressed against the set of z-score normalized environmental predictors. Normalization of environmental predictors facilitates comparison of effect size between predictors, such that regression betas reflect the change in the physiological parameter associated with a standard deviation change in each predictor. All combinations of linear models with no interaction terms were considered; the selected model minimizes the Bayesian Information Criterion (BIC), a measure of model fit that penalizes more complex models (Schwarz 1978). Assumptions of normality and linearity were assessed visually; White's test (White 1980) was used to test for heteroskedasticty.

Physiological parameters were also compared between mountains to assess differences in tree vigor at the population level using one-way analysis of variance, with significance established at the 0.05 confidence level. All data was assessed to ensure assumptions of normality and equality of variances were met. Differences between mountains were tested in a post-hoc test using Tukey's Honestly Significant Difference (HSD) criterion (Kramer, 1956), with significance again set at the 0.05 level.

4.3 Results

Summary statistics are reported for physiological measurements across all trees and environmental variables across all plots in Table 4.1.

Our attempts to reduce the dimensionality of diameter growth, A_{max}, WUE, root and stem NSC, SLA, and needle pigment content in adult Fraser fir to generate a comprehensive measurement of tree vigor and health were unsuccessful (Table 4.2). The first principle component only explains 27% of the variation, and it takes five components to explain 82 % of the variation in the data structure. With respect to the component loadings, the gas exchange measurements of A_{max} and WUE are loaded onto the first component and the leaf resource investment metrics of SLA and total chlorophyll on the second. Diameter growth, root NSC,

Table 4.1. Summary statistics of physiological measures from adult Fraser fir across 37 plots in Great Smoky Mountains National Park and corresponding plot scale environmental measurements from these plots.

Physiological measures	Median	Mean	Std. Dev.	N
Specific Leaf Area ($m^2 \cdot kg^{-1}$)	8.90	9.02	1.90	217
Carotenoids ($mg \cdot g^{-1}$)	0.07	0.07	0.04	217
Total Chlorophylls ($mg \cdot g^{-1}$)	2.02	2.10	0.63	217
Chlorophyll A ($mg \cdot g^{-1}$)	1.35	1.37	0.35	217
Chlorophyll B ($mg \cdot g^{-1}$)	0.68	0.73	0.31	217
A_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	0.88	1.09	0.61	177
Transpiration ($mmol \cdot m^{-2} \cdot s^{-1}$)	0.32	0.35	0.13	177
Water Use Efficiency ($\mu mol\ CO_2 \cdot mmol^{-1}\ H_2O$)	2.74	3.32	1.81	177
Root Starch (% dry mass)	4.10	4.28	1.32	217
Root Sugar (% dry mass)	43.47	43.80	12.31	217
Core Sugar (% dry mass)	1.36	1.54	0.94	217
Core Starch (% dry mass)	4.78	4.79	0.90	217
Root TNC (% dry mass)	47.95	48.08	12.56	217
Core TNC (% dry mass)	6.15	6.32	1.37	217
Diameter Growth (Δ cm $\cdot$ 10 yr^{-1})	4.90	5.57	3.09	217
Diameter at Breast Height (cm)	16.00	16.08	5.48	217

Environmental measures	Median	Mean	Std. Dev.	N
Mean Temperature (C)	8.13	8.21	0.20	37
Max July Temperature (C)	13.85	14.06	0.84	37
Degree Days	554	584	90.6	37
Sulfur ($kg \cdot ha^{-1} \cdot yr^{-1}$)	35.68	32.49	7.00	37
Nitrogen ($kg \cdot ha^{-1} \cdot yr^{-1}$)	26.60	24.09	5.36	37
Available Water Supply to 25 cm (cm)	3.55	4.74	2.24	37
Soil pH	3.50	3.57	0.29	37
P (ppm)	15.50	17.07	8.07	37
K (ppm)	57.00	61.89	20.40	37
Ca (ppm)	122.00	151.32	99.09	37
Mg (ppm)	35.50	38.27	13.03	37
Zn (ppm)	2.65	2.99	1.41	37
Mn (ppm)	6.50	12.93	15.25	37
Cu (ppm)	0.50	0.60	0.31	37
B (ppm)	0.55	0.56	0.26	37
Na (ppm)	38.50	40.59	11.24	37
Al (ppm)	336.04	418.63	269.88	37
CEC ($meq \cdot 100\ g^{-1}$)	15.30	15.40	2.46	37

Table 4.2. Results from Principal Components Analysis performed on physiological measurements from 222 adult Fraser fir (*Abies fraseri*) in Great Smoky Mountains National Park. Principle components were calculated as the eigenvectors of the pair-wise covariance matrix.

Physiological Metric	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Light-saturated Photosynthesis	0.56	0.35	-0.01	0.14	0.03	-0.18	-0.12	0.70
Photosynthetic Water Use Efficiency	0.51	0.46	-0.05	0.18	0.11	-0.08	0.07	-0.69
Total Chlorophyll	-0.33	0.50	-0.07	0.06	0.16	0.49	-0.61	0.02
Specific Leaf Area	-0.38	0.47	-0.19	0.14	0.12	0.07	0.73	0.17
Diameter Growth 2000-2010	0.19	-0.11	0.73	0.08	0.33	0.50	0.23	0.05
Root Nonstructural Carbohydrates	-0.18	-0.03	0.25	0.82	-0.47	-0.08	-0.07	-0.02
Core Nonstructural Carbohydrates	-.02	-0.37	-0.38	-0.49	0.68	-0.02	-0.06	0.02
Carotenoids	0.33	-0.20	-0.46	0.06	0.16	0.49	-0.61	0.02
Percent Explained	27.2	18.2	14.2	12.5	10.3	8.7	6.8	2.1
Cumulative Percent Explained	27.2	45.3	59.6	72.0	82.3	91.1	97.9	100

and stem NSC are loaded onto the third, fourth and fifth components respectively. Leaf carotenoid and chlorophyll content are the main parameters loaded onto the sixth principle component.

Results from the plot-wise ANOVAs performed using each of these physiological variables are given in Table 4.3; the R^2 values presented here are the proportion of variance in these response variables that is possible to be explained by plot-scale environmental parameters. These values are highest in the gas exchange measurements with 74% for A_{max} and 72% for WUE. While these proportions are smaller for diameter growth (58%), total needle chlorophyll (54%), total carotenoid amounts (49%), and SLA (43%), they are smallest for NSC values in both root and stem tissues (29% and 19%, respectively). This indicates that there is a large variation in non-structural carbohydrate storage between individuals in the same plot. Tree size was not a statistically significant explanatory variable for any of the physiological measurements.

Mean A_{max} (per plot) responded to elevation, percent slope, and soil Al (Table 4.4 A, total model $p = 0.0001$, $r^2=0.541$). All three environmental factors have a positive effect on plot mean A_{max}. Soil Al content and elevation having the strongest effects; percent slope having half the effect size of that of elevation. Examining projected A_{max} over an elevational gradient, a 200 meter increase in elevation raises predicted mean A_{max} by 0.5 $\mu mols \cdot m^{-2} \cdot s^{-1}$ (Figure 4.1). Incorporating the water cost of carbon fixation as WUE, we see that Mean WUE (per plot)

Table 4.3. Results of plot-wise one-way ANOVAs performed on physiological measurements from 222 adult Fraser fir (*Abies fraseri*) at 37 plots in Great Smoky Mountains National Park. R^2 values presented show the amount of variation in the measurements explainable by the plot label. All tests were significant at the alpha=0.05 level.

Physiological Metric	R^2 value
Light-saturated Photosynthesis (A_{max})	0.74
Photosynthetic Water Use Efficiency	0.72
Diameter Growth	0.58
Chlorophyll Content	0.54
Carotenoid Content	0.49
Specific Leaf Area	0.42
Root Non-structural Carbohydrates	0.29
Core Non-structural Carbohydrates	0.19

responded to percent slope , Max July Temp, and CEC (Table 4.4 B whole model p = 0.00446, r2=0.39). While percent slope has a positive effect on WUE, both maximum July temperature and soil cation exchange capacity have a negative effect. When examining predicted mean WUE in terms of maximum July temperatures, a 3 C increase in max July temperatures results in a decrease of photosynthetic WUE from 4 μmol $CO_2 \cdot mmol^{-1}$ H_2O to 2 μmol $CO_2 \cdot mmol^{-1}$ H_2O (Figure 4.2).

In terms of all physiological response variables measured, regression models for SLA highest predictive value. Mean SLA (per plot) responded to Max July Temp, K, and CEC (Table 4.4 C whole model p < 0.00001, r2=0.633). Soil CEC had a positive effect on fir needle SLA, and soil K had a negative effect (Table 4.4 C). Increases in Max July Temp had the largest effect on predicted mean SLA (per plot), with a 3 C increase in summer temperatures yielding an increase in 2 m2/kg (Figure 4.3). Plot mean chlorophyll amount in needles is negatively correlated with acidic deposition (Table 4.4 D whole model p < 0.00013, r2=0.346).

With regard to end of season NSC storage pools, we found much greater levels in root tissue as compared to stem tissue, most of which is expressed in sugars (Table 4.1). Mean Root NSC (per plot) responded positively to max July temperature, with generally higher sugar storage in end of season root tissue in plots with higher summer temperatures (Table 4.4 E, p=0.00318, r2=0.223). This relationship is fairly weak, however, with a 3 C temperature increase

Table 4.4. Linear regression models to predict plot-mean physiological measurements from adult Fraser fir (*Abies fraseri*) in Great Smoky Mountains National Park. Models were selected using the Bayesian Inference Criterion.

A. $A_{max} = I + Elevation + Slope + Al$

	Estimate	SE	tStat	p-value
(Intercept)	1.0591	0.071769	14.757	3.7738e-14
Elevation	0.26684	0.070197	3.8013	0.00078319
Slope	0.13237	0.068704	1.9267	0.045012
Al (in ppm)	0.2968	0.073814	4.0209	0.00044274

n: 30, error df: 26, RMSE: 0381, R^2: 0.54, F-stat vs. constant model: 10.2, $p < 0.001$

B. *WUE = I + Slope + Max July Temp + CEC*

	Estimate	SE	tStat	p-value
(Intercept)	3.2666	0.24704	13.223	4.7403e-13
Slope	0.78372	0.24468	3.203	0.0035759
Max July Temp	-0.69415	0.23732	-2.9249	0.0070566
CEC	-0.54201	0.27124	-1.9983	0.046244

n: 30, error df: 26, RMSE: 1.29, R^2:0.39, F-stat vs. constant model: 5.54, $p < 0.005$

C. *SLA = I + Max July Temp + K + CEC*

	Estimate	SE	tStat	p-value
(Intercept)	8.9996	0.13051	68.959	2.973e-37
Max July Temp	0.92319	0.13576	6.8001	9.347e-8
K	-0.49523	0.17476	-2.8337	0.0077893
CEC	0.43259	0.1762	2.4551	0.019524

n: 37, error df: 33, RMSE: 0.794, R^2: 0.633, F-stat vs. constant model: 18.9, $p < 0.001$

D. *Total Chlorophyll = I + Acid Deposition*

	Estimate	SE	tStat	p-value
(Intercept)	208.9	6.3408	32.946	6.169e-28
Acid Dep	-27.646	6.4283	-4.3006	0.00012974

n: 37, error df: 35, RMSE: 38.6, R^2: 0.346, F-stat vs. constant model: 18.5, $p < 0.001$

E. *Root NSC = I + Max July Temp*

	Estimate	SE	tStat	p-value
(Intercept)	48.049	1.0001	48.046	1.5092e-33
Max July Temp	3.2118	1.0139	3.1679	0.0031799

n: 37, error df: 35, RMSE: 6.09, R^2: 0.223, F-stat vs. constant model: 10.0, $p < 0.001$

yielding a predicted increase from 45 % to 55% of root NSC by weight (Figure 4.4). We find there is limited predictive power of plot-level environmental data on NSC in either root or stem tissue, and wide within-plot variation in carbon storage pools.

The remaining regression models for needle carotenoid content, diameter growth, and core NSCs are reported in the Appendix.

When comparing gas exchange measurements between mountains, we find that trees on Clingmans Dome had significantly higher A_{max} than those on other mountains; mean A_{max} was twice as high on this mountain than average A_{max} of trees at other locations (Figure 4.5). When considering the transpiration cost of carbon fixation as water use efficiency, again trees on Clingmans Dome perform significantly better than those on other mountains (Figure 4.6). These higher rates of carbon fixation are not explained by increases in needle photosynthetic pigment (Figure 4.7) when viewed on the same scale, trees with highest A_{max} have about half the total chlorophyll amounts of those with the most concentrated pigment levels.

To determine whether trees on certain mountains had smaller NSC pools, we compared the size of these pools in root tissue between mountains. While results show significant differences between mean carbohydrate content (expressed as % dry weight) from Mount Collins and Clingmans Dome (Figure 4.8), differences are not appreciable.

4.4 Discussion

We measured key physiological parameters associated with carbon gain and storage in adult Fraser fir in threatened high-elevation cloud forests. Though these measurements contribute to tree health and stress tolerance, our study shows that, in Fraser fir, they are not highly correlated. Individual trees rarely performed highly with respect to more than one metric, suggesting that individuals dealt with the stresses they encountered in different ways. There is high uncorrelated variation between individuals; conservation targets should be selected to conserve this phenotypic diversity within the species.

Additionally, though we have quantified some measures of carbon gain, storage and growth, we do not have measurements of carbon costs for dark respiration, reproduction or defense, nor whole-day or whole-year estimates of photosynthesis, and these measurements

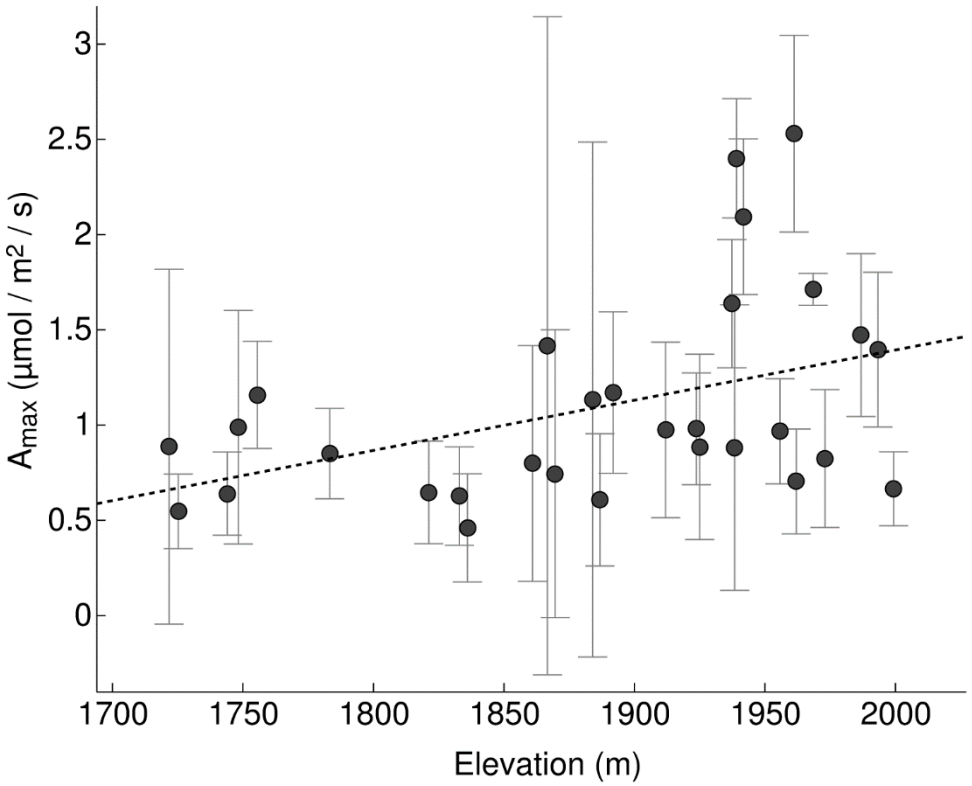

Figure 4.1. Plot-mean light-saturated photosynthesis rates from 180 adult Fraser fir (*Abies fraseri*) at 30 sites in Great Smoky Mountains National Park regressed against plot elevation. Dots represent site means, bars represent the 80% prediction interval. The full regression model is given in Table 4.4 A.

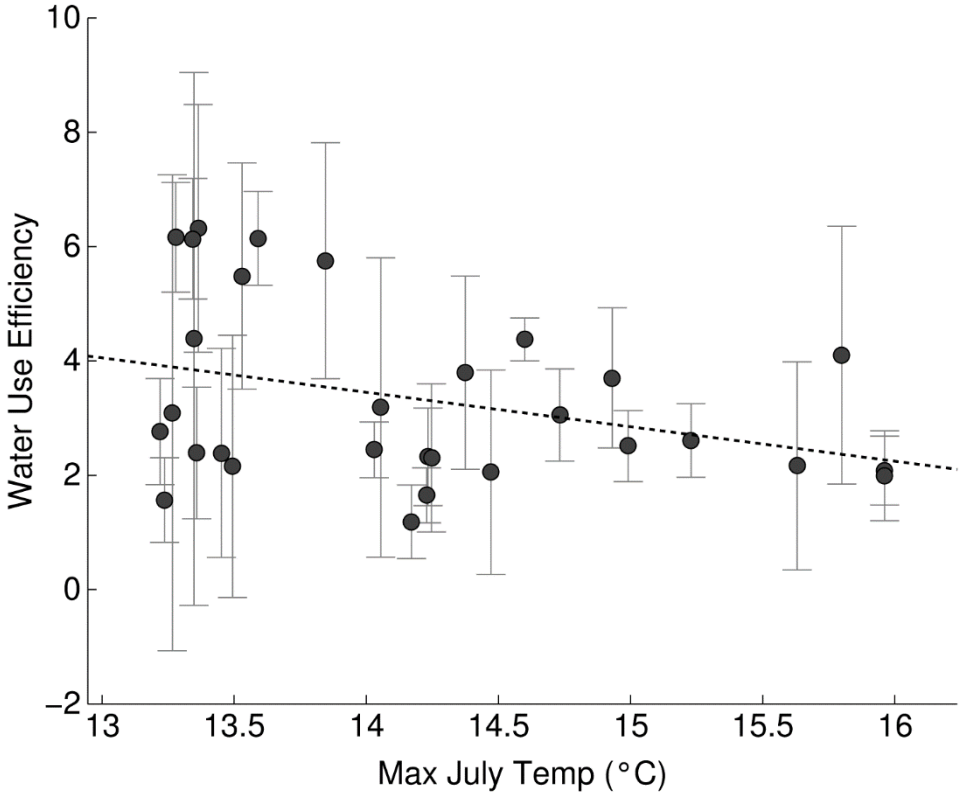

Figure 4.2. Plot-mean photosynthetic water use efficiencies from 180 adult Fraser fir (*Abies fraseri*) at 30 sites in Great Smoky Mountains National Park regressed against plot maximum July temperatures (from Fridley 2009). Dots represent plot means, bars represent the 80% prediction interval. The full regression model is given in Table 4.4 B.

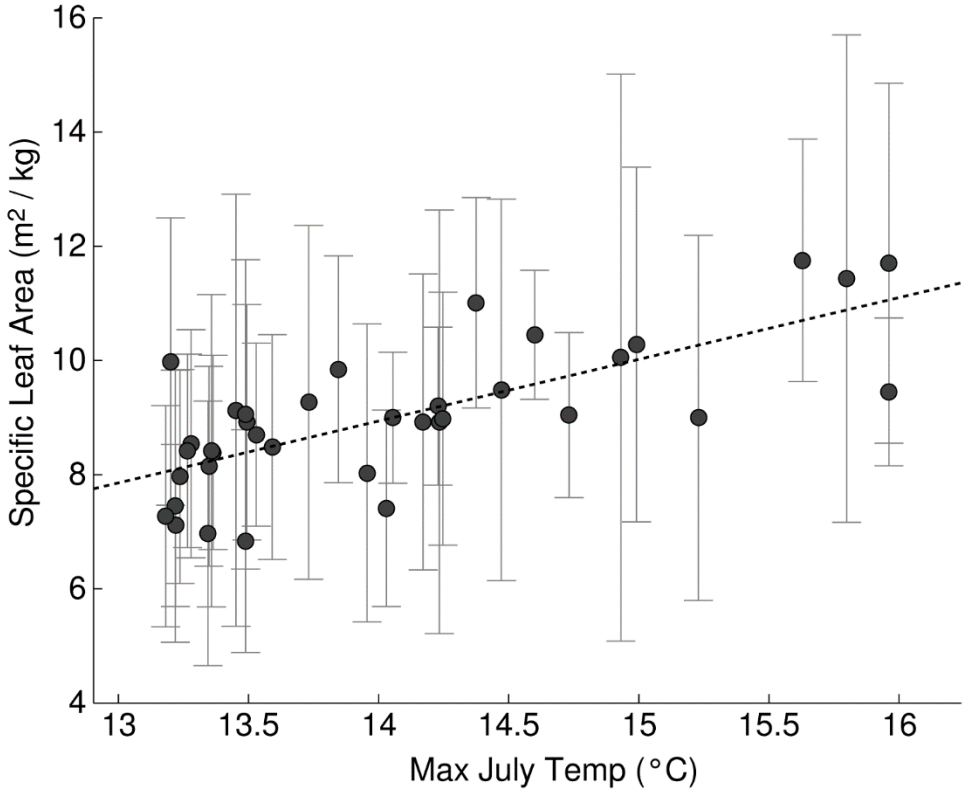

Figure 4.3. Plot-mean specific leaf areas from 217 adult Fraser fir (*Abies fraseri*) at 37 sites in Great Smoky Mountains National Park regressed against site maximum July temperatures (from Fridley 2009). Dots represent plot means, bars represent the 80% prediction interval. The full regression model is give in Table 4.4 C.

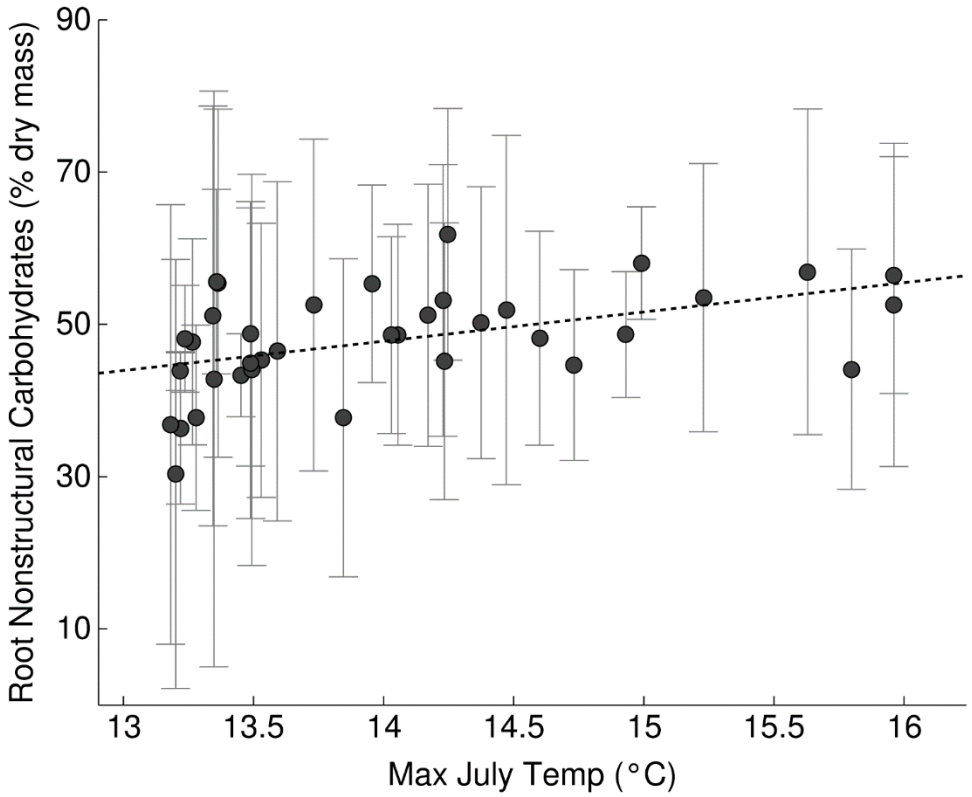

Figure 4.4. Plot-mean root nonstructural carbohydrate amounts (as % dry mass) from 217 adult Fraser fir (*Abies fraseri*) at 37 sites in Great Smoky Mountains National Park regressed against site maximum July temperatures (from Fridley 2009). Data are the sum of simple sugar and starch pools. Dots represent plot means, bars represent the 80% prediction interval. The full regression model is given in Table 4.4 E.

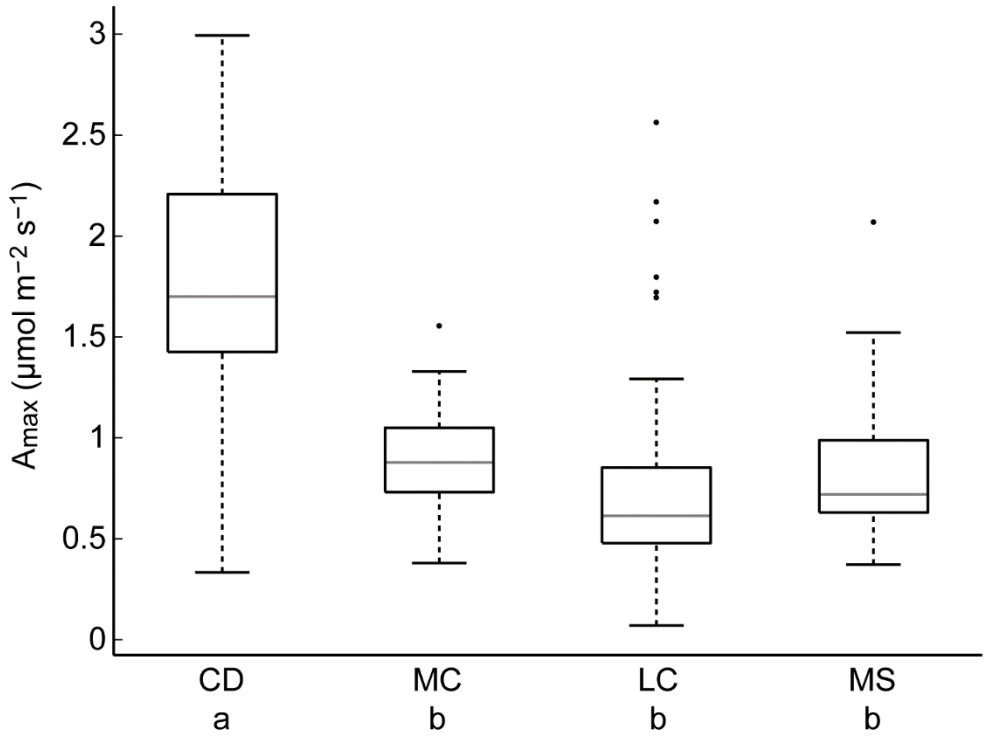

Figure 4.5. Box plot of light-saturated photosynthesis rates in adult Fraser fir (*Abies fraseri*) compared between mountains (Clingmans Dome - CD, Mount Collins - MC, Mount LeConte – LC, Mount Sterling – MS). The central mark represents the median value, edges of the box are the 75th and 25th percentiles, whiskers extend to the most extreme values that are not an outlier, outliers are defined as points that fall outside of +/- 1.5 times the interquartile range. Letters under mountains designate significant difference at alpha=0.05 using Tukey's H.S.D.

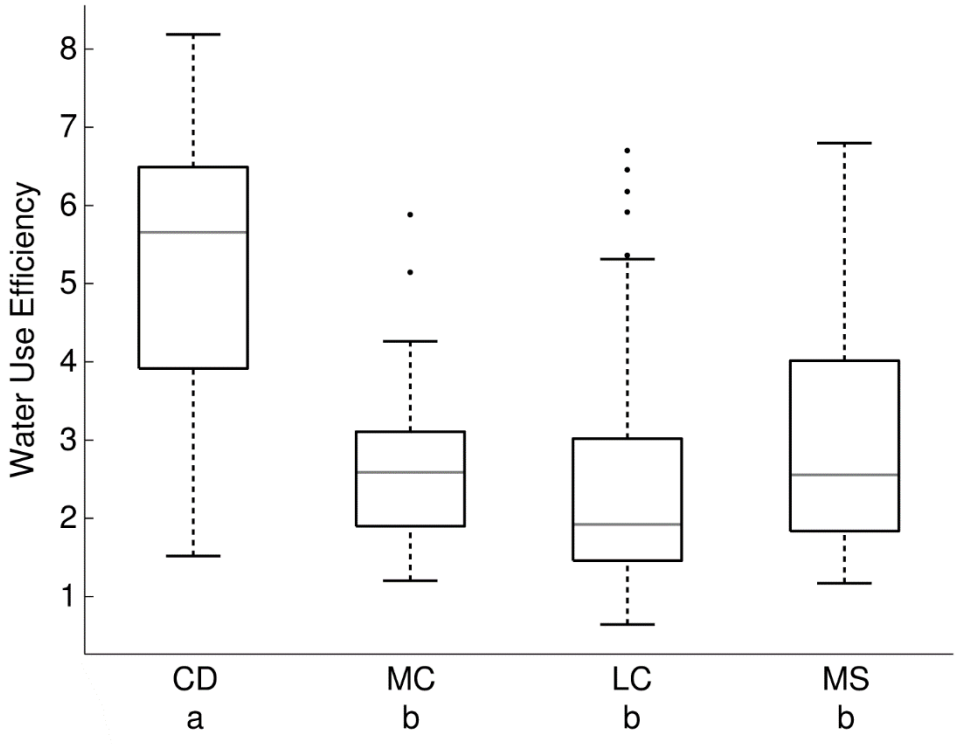

Figure 4.6. Box plot of photosynthetic water use efficiencies in adult Fraser fir (*Abies fraseri*) compared between mountains (Clingmans Dome - CD, Mount Collins - MC, Mount LeConte – LC, Mount Sterling – MS). The central mark represents the median value, edges of the box are the 75th and 25th percentiles, whiskers extend to the most extreme values that are not an outlier, outliers are defined as points that fall outside of +/- 1.5 times the interquartile range. Letters under mountains designate significant difference at alpha=0.05 using Tukey's H.S.D.

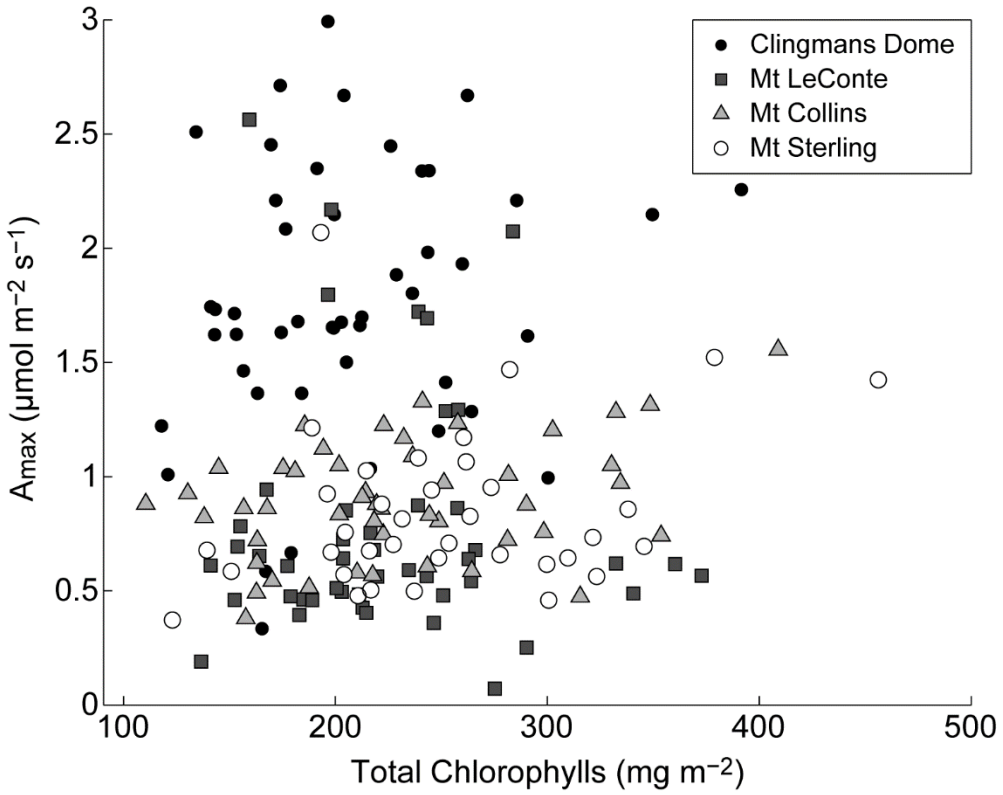

Figure 4.7. Scatterplot of light saturated photosynthetic rates and total leaf chlorophyll amounts (A+B) from 217 adult Fraser fir (*Abies fraseri*) in Great Smoky Mountains National Park. Values are expressed in terms of leaf area. Symbols represent trees on Clingman's Dome (closed circle), Mount LeConte (gray square), Mount Collins (gray triangle), and Mount Sterling (open circle).

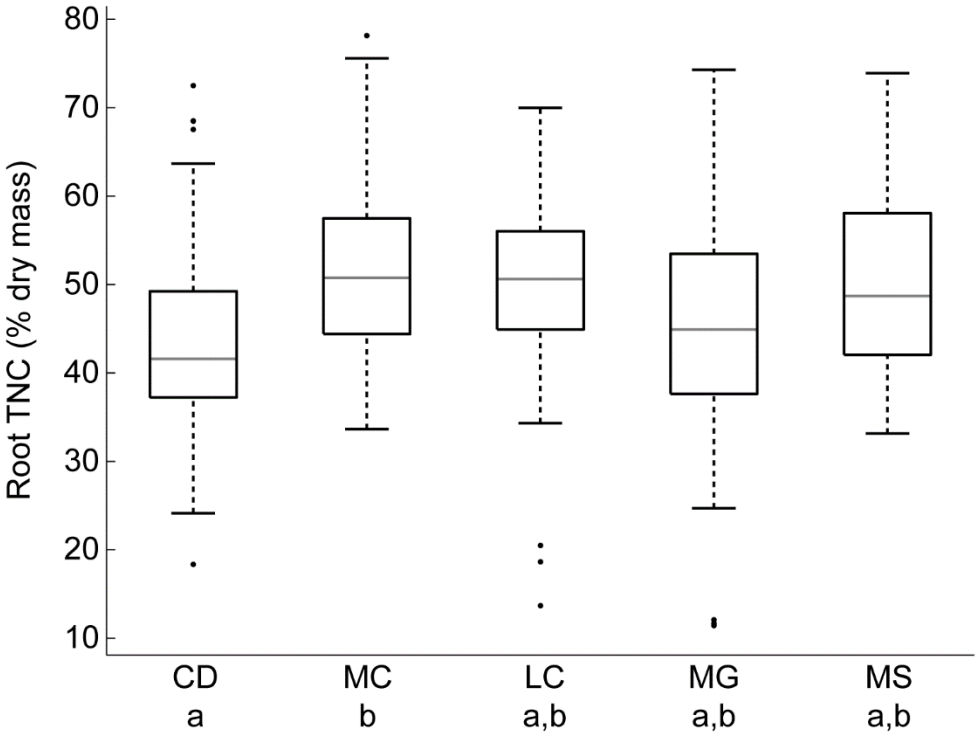

Figure 4.8. Box plot of total nonstructural carbohydrates (simple sugar + starch) in root tissue adult Fraser fir (*Abies fraseri*) compared between mountains (Clingmans Dome - CD, Mount Collins - MC, Mount LeConte – LC, Mount Guyot – MG, Mount Sterling – MS) expressed as % dry mass. The central mark represents the median value, edges of the box are the 75th and 25th percentiles, whiskers extend to the most extreme values that are not an outlier, outliers are defined as points that fall outside of +/- 1.5 times the interquartile range. Letters under mountains designate significant difference at alpha=0.05 using Tukey's H.S.D.

would clarify estimates of whole tree carbon budgets. Shoot physiology integrated over the entire crown of the tree may help explain limitations in carbon fixation and observed decline in health and vigor in Fraser fir.

Our study has defined an upper bound on the variability in physiological measurements that is explainable by site level environmental parameters. The remaining within-plot variability comes from history, genetics, microbiome and measurement error. Though tree size was not a significant factor in any of the physiological measurements, tree age (and thus, tree history) may be. Fraser fir is a shade-tolerant slow-growing species which can persist in the understory many years before canopy release (Oosting and Billings 1951), and tree age and size are not well correlated in these stands (Mancusi 2004). Common garden experiments may be a useful approach to control for these factors, but, in Fraser fir, this method is limited by the slow growth and long life cycle of firs.

Maximum photosynthetic rates in adult Fraser fir were highest at the highest and steepest sites, and trees in these stands may be more resistant to future chronic and episodic stress than trees at the lower bounds of the elevation range. Our measurements of A_{max} are lower than those given by Reinhardt et al. (2009), who reports an average A_{max} of 3.0 ± 0.2 $\mu mols \cdot m^{-2} \cdot s^{-1}$ for adult Fraser fir understory trees, and Bernier et al. (2001) who found average A_{max} of 4.3 $\mu mols \cdot m^{-2} \cdot s^{-1}$ for adult understory balsam fir (*Abies balsamea*). However, similar species to Fraser fir which are facing multiple stresses or are in decline have comparable A_{max} (Zimmermann et al. 1988; Johnson et al. 2004).

The positive relationship between A_{max} and soil aluminum levels was unexpected. However, other studies have found that moderate amounts of aluminum are correlated with peak growth rates (McCanny et al. 1995) and increases in photosynthetic rates (McLaughlin et al. 1991) in red spruce, a co-dominant species which is more sensitive to aluminum toxicity than fir (Schier 1985). It has been hypothesized that Al exerts a positive effect on red spruce at field concentrations (McCanny et al. 1995), and our data suggests that this may also be true in Fraser fir.

Though the large amounts of individual variation that can possibly be explained by plot-level environment we have reported for gas exchange measurements (A_{max} 74%, WUE 72%) may be partially attributed to preceding weather patterns between plots, the regression models built

were able to explain a large portion of the variation in these measurements (A_{max} 54%, WUE 39%).

Here we explored environmental constraints on fir physiology. While the biological relevance of some of the regression models is not readily apparent, particularly with regard to the model presented for light saturated photosynthesis, we can offer some thought on why these variables may be preferred to more mechanistic variables. Model selection conservatively picks the most explanatory variables, therefore there is at minimum more information contained in elevation than simply water availability and temperature, which are not included in the model. Alternatively elevation succinctly summarizes the information included in those two variables, making their inclusion redundant.

For both A_{max} and WUE in Fraser fir, soil available water supply was not a significant predictor variable. Cloud immersion has been shown to be vitally important to fir water relations, with up to one third of plant water absorbed by needles from clouds (Berry and Smith 2014). Elevation and percent slope may instead explain this vital, but here unmeasured, variable. Additionally, measurements of A_{max} are shown to be significantly higher at Clingmans Dome which also may contribute to the high predictability of elevation and percent slope.

Our predictive models for specific leaf area highlight the importance of nutrient availability and temperature in determining leaf architecture. SLA is a measure of plant investment of carbon to light-intercepting leaf area per unit leaf dry mass, and is a key trait in the carbon economy of a plant (Wright et al. 2004; Reich et al. 2007). A relatively high SLA allows for greater carbon uptake and relative growth rate in the short term, and is observed in leaves of younger compared to older trees (Day et al. 2001; Thomas and Winner 2002). A low SLA may be an adaptive trait to cope with climatic stress in cold environments, and has been observed to decrease with increasing elevation in adult conifers (Hultine and Marshall 2000). We find that higher maximum July temperature increases SLA in Fraser fir, which implies an increase in resource investment in photosynthetic machinery under future warming.

Acidic deposition was only found to have a significant negative impact with regard to needle chlorophyll levels in Fraser fir. Acid deposition is well known to disrupt tree nutrient availability and causes through-fall and leaching in needles (Aber et al. 1989; Lucier and Haines

1990; Eagar and Adams 1992; Johnson and Lindberg 1992), and our findings are consistent with the body of scientific literature.

In contrast to foliar measurements of carbon acquisition, carbon storage is not well predicted by environmental variables and is highly variable between individuals. Given the broad spectrum of relationships between NSC to other physiological processes, there are many sources of variation in the NSC pool. NSC levels in Fraser fir may vary because of environmental stress on carbon source-sink balance (Kozlowski 1992), or may result from active accumulation of carbon stores for coping with long periods of freezing temperatures. Because our data shows a low ability to predict the size of NSC pools, it suggests that these pools are not solely controlled by environmental stressors. Instead, between tree differences may be the result of different fixation rates and differences in carbon demand from respiration, growth or reproduction, which taken together may define carbon usage strategies for different individuals.

The size of NSC pools is a critical factor in tree survival through periods of environmental stresses by directly covering metabolic needs and fueling structural and metabolic acclimation to additional stresses (Amthor and McCree 1990). In general, our measurements of the size of NSC pools in Fraser fir are consistent with those found in mature trees of other species (Hoch et al. 2003; Hoch and Körner 2009; Richardson et al. 2013). This suggests that high-elevation forests may have the capacity for resistance of future stress events, particularly at the highest elevations where photosynthetic rates are the highest. Additionally, we find that the end of season is highest in the root tissue and mostly in the form of sugars, which may increase osmotic water gain as the ground freezes in these high elevation montane forests.

Delcourt and Delcourt (1998) predicted that a 3 C increase in the mean July temperature would result in the loss of Fraser fir forests. While the current study examines the effect of maximum July temperatures on Fraser fir forests, it does cover a 3 C range which we find results in significant decreases in photosynthetic WUE. Higher maximum July temperatures are correlated with increases in SLA, meaning needles are flatter and thinner. However, our data finds no strong effect on light-saturated photosynthetic rates, which, coupled with the increases in photosynthetic water cost and shifts in leaf architecture, suggests decreases in the efficiency of carbon fixation at higher summer temperatures. Recent studies have shown that the effect of temperature on leaf-level VPD and water demand are mitigated by cloud immersion in

understory Fraser fir (Johnson and Smith 2006; Berry and Smith 2012; Berry and Smith 2013). In Southern Appalachian fir forests, where rates of carbon fixation are already low, we hypothesize that future warming will restrict Fraser fir occurrence to the highest elevations and cloud-dense areas.

This study finds that, on the basis of foliar physiology, trees at Clingmans Dome perform better than trees at other sites. This is not simply due to higher photosynthetic pigment content; indeed these trees have considerably lower pigment levels than trees with lower photosynthetic rates found at other sites. This may indicate a breakdown in biochemical efficiency at other sites, or evidence of genetic or phenotypic stress resistance in trees at Clingmans Dome. Further study is warranted.

Finally, while the present study examined carbon dynamics in trees under multiple stresses and the direction and effect size of environmental conditions on fir physiology, we did not examine interactive effects between environmental parameters. The sequence, severity, and duration of stresses may change overall tree response and the extent to which trees can acclimate and persist in systems with multiple stresses (Aber et al. 2001; Niinemets 2010). Here, we have asked what the environmental constraints on fir physiology are. However, physiological metrics are also themselves causally related. Explicitly mechanistic approaches such as structural equation modeling or hierarchical Bayesian methods may be an appropriate way to incorporate stress interactions and timing and causal relationships between physiological variables.

4.5 Conclusions

Physiological measurements associated with carbon gain, use and storage in mature Fraser fir cannot be collapsed into a simplistic health score, and, on average, roughly half of the variability in these measurements can be explained by site level environmental measurements. This study is the first to examine carbon gain and carbohydrate pools in adult Fraser fir trees and to link environmental conditions to these measurements *in situ*. Maximum photosynthetic rates are low throughout the high elevation mountains of Great Smoky Mountains National Park, indicating trees are under considerable stress, but are highest in trees growing on the highest, steepest slopes. Trees from Clingmans Dome have significantly higher maximum

photosynthetic rates and water use efficiency, which may indicate stress resistance in this population. Maximum July temperature plays an important role in the water use efficiency and needle specific leaf area in Fraser fir. Future warming is likely to restrict Fraser fir occurrence to the highest elevations and cloud-dense areas. Questions about whether resistance to multiple stresses at these sites is genetically controlled, or the result of phenotypic plasticity, or is explained by unmeasured environmental parameters still remain.

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Appendix

Linear regression models to predict plot-mean physiological measurements from adult Fraser fir (*Abies fraseri*) in Great Smoky Mountains National Park. Models were selected using the Bayesian Inference Criterion.

A. *Carotenoids = I + Mean Temp + Max July Temp*

	Estimate	SE	tStat	p-value
(Intercept)	7.1095	0.40606	17.508	1.3889e-18
Mean Temp	1.2483	0.63636	1.9616	0.04804
Max July Temp	-2.711	0.63636	-4.2602	0.00015269

n: 37, error df: 34, RMSE: 2.47, R^2: 0.394, F-stat vs. constant model: 11.1, $p < 0.001$

B. *Core NSC = I + P*

	Estimate	SE	tStat	p-value
(Intercept)	6.3241	0.090834	69.631	3.9512e-39
P	0.27035	0.092076	2.9362	0.005838

n: 37, error df: 35, RMSE: 0.552, R^2: 0.198, F-stat vs. constant model: 8.62, $p < 0.01$

C. *Diameter Growth = I + K + Ca*

	Estimate	SE	tStat	p-value
(Intercept)	5.536	0.32455	17.058	3.0866e-18
K	1.893	0.44664	4.2384	0.00016269
Ca	-1.1434	0.44664	-2.56	0.015081

n: 37, error df: 34, RMSE: 1.97, R^2: 0.348, F-stat vs. constant model: 9.07, $p < 0.001$

Chapter 5
Conclusions

The previous chapters, taken as a whole, provide some broad patterns and insights into the dynamics and persistence of high elevation spruce-fir forests in the southern Appalachians. They also address previously unexamined questions about carbon fixation in adult Fraser fir trees *in situ* as well as providing valuable predictions of both the future of this endemic species and threatened forest type in the coming decades. Additionally, there are clear and valuable implications for forest management relevant for the conservation and restoration of spruce-fir forests. Furthermore, long term monitoring and collection of baseline data on forest health is an important goal, and the data collected and contained in the previous chapters is a significant contribution to long-term ecological research.

We find no regular, consistent increase in hardwood share in high elevation forests (Chapter 2), but predict further declines in fir populations, particularly at Mount Sterling (Chapter 3). Together these studies suggest that the once dense spruce-fir forests will be replaced with novel ecosystems. Observations from the field during data collection indicate fern brakes, grassy balds, and shub thickets dominated by *Rubus canadensis* are likely replacements. Studies by Crandall (1958) and Busing et al. (1988) both indicate that the establishment of fern brakes and *Rubus* thickets are common in canopy gaps created by individual tree mortality. However, because of the wide-spread extent of fir overstory mortality, seed sources may be lacking to regenerate spruce-fir forests in these areas. Thus, difference in scale between the patch sizes created by single tree mortality and large scale overstory mortality may be an important driver in land cover changes. Further, studies have shown that high cover of *Rubus canadensis* is associated with low fir seedling density (Pauley and Clebsch 1990; Pauley 1989); competition may be limiting forest re-establishment in these patches.

This dissertation also finds that data at two different scales corroborate one another. Leaf level physiological metrics (Chapter 4) and results from our fir population model (Chapter 3) both suggest that Fraser fir trees at Clingmans Dome possess some measure of resistance to chronic environmental stresses. Varying response to stress in plants from a single location is not unlikely. A study of elevated warming effects on another high-elevation Southern Appalachian species, red spruce, found varying response to increased temperatures among different seed sources (Hagen 2006). In Fraser fir, Li et al (1988) found differences in seedling growth rates and biomass production from seeds from different elevations. A study of population genetics in Fraser fir found small but significant differences between allele number, allele richness and

allele privacy between different populations (Potter et al. 2008). Though our data indicates that stress resistance in the Clingmans Dome population is likely, it is unknown if this is due to phenotypic plasticity or genetically controlled, and further study is warranted.

Additionally, our data suggests that management strategies which protect a number of adult trees will yield faster forest regeneration, presumably due to the presence of ready seed sources (Chapter 3). However, our characterization of ecophysiological measurements in fir indicate that the selection of individual trees for targeted managing efforts or future conservation may be not a straightforward matter (Chapter 4). Physiological measurements associated with leaf resource investment, carbon fixation rates, carbon storage pools and growth were found to be largely uncorrelated with one another in adult Fraser fir. Even when examining a single metric, light—saturated photosynthesis rates, we find a few individuals trees with higher rates in plots dominated by trees with much lower rates (Figure 4.7). While tree physiology is only partially controlled by genetics, this dissertation supports a general biological principle that diversity within populations is important.

Recent work in tree ecophysiology have called for measurements of NSC pools, especially under environmental stresses (Adams et al. 2009; Leuzinger et al. 2009; Sala 2009; McDowell & Sevanto 2010; Sala et al., 2010). These pools, which are not often quantified, are thought to allow trees to persist through stress events by covering both maintenance carbon costs as well as providing carbon for biochemical compounds that provide mechanisms of resistance. Our data adds to body of scientific knowledge on this front. Additionally, though a number of studies have posited the carbon starvation hypothesis as a mechanism for tree mortality (McDowell & Sevanto 2010; Adams et al. 2009), our data suggests that carbon starvation isn't responsible for the observed declining vigor of Fraser fir trees, and instead other factors, such as disruptions to water relations or biochemical pathways, may be to blame.

Lastly, a recent paper by McNulty et al. (2014) posits that changes in climatic variability may cause what they term “the rise of the mediocre forest”. They hypothesize that chronically stressed trees may be better suited to survive the combination of chronic low-level environmental stress and extreme episodic stress associated with anthropogenic climate change and increasing climate variability. These conditions may create a selection bias toward individuals that have persisted through chronic stress events over their non-stressed, vigorous

conspecifics. The studies presented here establish important baseline data for both monitoring this threatened forest as well as testing the mediocre forest hypothesis in the coming decades.

A number of ideas for future study have arisen in the course of completing this dissertation. Though we did not address specifically mechanistic models in Chapter 4 or examine specific interactions between environmental variables or causal relationships between physiological metrics, applying hierarchical Bayesian modeling or structural equation modeling to datasets generated and used in chapter 4 may be a next step. Applying statistical clustering methods to group particularly vigorous tress, which may highlight broad physiological strategies in adult Fraser fir, could also follow. In the course of this work, a large data set of needle morphology metrics was generated. Preliminary analysis shows that stunted needles have proportionally fewer non-photosynthetic compounds than healthy needles, suggesting that stressed trees prioritize photosynthetic capacity over secondary functions performed by other compounds. We would like to incorporate the temperature gradients from chapter 4 as well as soil nutrient measurements into this analysis. Lastly, though common garden experiments are difficult undertakings with slow growing species like Fraser fir, we recently discovered that NPS started a genetic conservation forest using Fraser fir in the mid-1990's. Future work could exploit this common garden to continue to study the effects of environment and role of genetics on Fraser fir physiology.

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Vita

Steven Douglas (Doug) Kaylor was born in Jonesboro, AR on March 26, 1981. He grew up in the mountains of northwest Georgia and spent his summers camping throughout the state; he climbed Clingmans Dome for the first (of many) time at the age of five. As a child, he learned the basics of plant biology and identification from his father, who was a high school agriculture instructor. He graduated from Chattooga High School in 1999 and went on to study Biology at Shorter College in Rome, GA where he earned his BS in the discipline in 2003 with honors. His honors thesis research project was the feeding periodicity and diet of southern two-lined salamander larvae. After graduation, he was a research fellow at Jug Bay Wetland Sanctuary in Maryland before pursuing a Master of Science degree at Marshall University. While there, his research focused on population modeling and habitat use of winter breeding Ambystomatid salamanders in a forested seasonal wetland, under the esteemed conservation herpetologist, Dr. Tom Pauley. Doug graduated from Marshall in December of 2006 and worked as a contract biologist in West Virginia before moving to Knoxville in 2009. He decided to switch his research focus to plant biology and accepted a research fellowship at the University of Tennessee, Knoxville, in the Tennessee Tree Physiology Lab in 2010. He earned a doctorate in Natural Resources in 2015 with a dissertation titled "Population Dynamics and Ecophysiology of Fraser fir (*Abies fraseri*) in High Elevation Forests in the Southern Appalachian Mountains." In addition, he completed a number of side projects on forest disturbance while at UTK. He is currently finishing a research internship at Oak Ridge National Laboratory examining climate warming effects on plant functional groups and nutrient pools in the Alaskan tundra.